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Early-Life-History Profiles, Seasonal Abundance, and Distribution of Four Species of Clupeid Larvae from the Northern Gulf of Mexico, 1982 and 1983

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Early-Life-History Profiles, Seasonal Abundance, and Distribution of Four Species of Clupeid Larvae from the Northern Gulf of Mexico, 1982 and 1983

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ABSTRACT

We present data on ichthyoplankton distribution, abundance, and seasonality and supporting environmental information for four species of coastal pelagics from the family Clupeidae: round herring *Etrumeus teres*, scaled sardine *Harengula jaguana*, Atlantic thread herring *Opisthonema oglinum*, and Spanish sardine *Sardinella aurita*. Data are from 1982 and 1983 cruises across the northern Gulf of Mexico sponsored by the South-eastern Area Monitoring and Assessment Program (SEAMAP). This is the first such examination for these species on a multi-year and gulfwide scale. Bioprofiles on reproductive biology, early life history, meristics, adult distribution, and fisheries characteristics are also presented for these species.

During the summer, larval Atlantic thread herring and scaled and Spanish sardines were abundant on the inner shelf (<40 m depth), but were rare or absent in deeper waters. Scaled sardine and thread herring were found virtually everywhere inner-shelf waters were sampled, but Spanish sardines were rare in the north-central Gulf. During 1982, larval Atlantic thread herring were the most abundant of the four target clupeid species, whereas Spanish sardine were the most abundant during 1983. On the west Florida shelf, Spanish sardine dominated larval clupeid populations both years. Scaled sardine larvae were the least abundant of the four species both years, but were still captured in 25% of inner-shelf bongo net collections. Round herring larvae, collected February–early June (primarily March–April), were abundant on the outer shelf (40–182 m depth) and especially off Louisiana. Over the 2-year period, outer-shelf mean abundance for round herring was 40.2 larvae/10 m²; inner-shelf mean abundances for scaled sardine, Atlantic thread herring, and Spanish sardine were 14.9, 39.2, and 41.9 larvae/10 m², respectively.

Introduction

The apparent abundance of clupeids in the eastern Gulf of Mexico and their potential for commercial fisheries have been well documented (Bullis and Thompson 1967, 1970; Bullis and Carpenter 1968; Fuss et al. 1969; Klima 1971; Wise 1972; Houde 1973, 1977b). The abundance of some of these stocks may even exceed that of gulf menhaden *Brevoortia patronus* (Bullis and Carpenter 1968). Houde (1975:73) has identified the sardine-like fishes, which include the four species of Clupeidae covered in this report, as abundant enough in the eastern Gulf to "... add significantly to the gulf menhaden fishery, and thus make valuable contributions to fishmeal and oil production in the United States." Some of the species are already lightly exploited, and most are heavily utilized in other parts of the world. In the United States these species could have commercial and recreational value as food fish, bait fish, oil reduction fish, and forage fish.

As forage fish, these species constitute an important, if not primary, food source for many predatory game and commercial fishes and may therefore directly affect the biomass of these predators. Other available forage fish may not be as abundant throughout their geographical range, reach high enough schooling densities, or have the same energy (oil) content or palatability as these species (Reintjes 1979a).

Given the important role that such coastal pelagics as the clupeids play in food chain dynamics and their potential as a latent resource, it is surprising that we do not presently know enough about them to accurately assess the extent to which they can be feasibly exploited (Nakamura 1980). This inadequacy is especially apparent in our understanding of the early-life-history stages. Knowledge about the welfare of the larval stage is crucial because two important determinants of recruitment and year-class strength are the magnitude of offshore reproductive success coupled with survival and growth of larvae at sea, within the coastal zone, or the estuarine nursery area.

This research was undertaken to augment the information on early life history of four coastal herrings: Atlantic thread herring *Opisthonema oglinum*, Spanish sardine *Sardinella aurita*, scaled sardine *Harengula jaguana*, and round herring *Etrumeus teres*. This is especially important in light of (1) the increasing awareness that some of our fisheries may be approaching, or may have already reached, their maximum sustainable yields; (2) today's political and economic climate with its justifiable emphasis on creating new job opportunities, utilizing untapped renewable resources, and balancing the international trade deficit; and (3) the appreciation of each Gulf state's need to develop, maximize, effectively manage, and partition fishery resources while minimizing conflicts between commercial and recreational users. Information provided in this report should help solidify the data foundation necessary for sound management of the Gulf's "fisheries of the future."

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Table 1
Summary of 1982 SEAMAP ichthyoplankton sampling in the northern Gulf of Mexico.

Vessel or state	Cruise	Dates	Station no.	Sample no.	Gear	Location
<i>Oregon II</i>	125	02/24-03/18	36005-36620	869-963	Bongo	Mississippi delta area
<i>Oregon II</i>	126	04/15-05/25	36659-36787	1-390	Bongo/Neuston	Gulfwide, offshore
<i>Bellows</i>	S482	04/27-04/29	01-08	391-414	Bongo/Neuston	Southwest Florida, offshore
<i>Hernan Cortez</i>	01	05/16-05/19	05-11	710-730	Bongo/Neuston	Southwest Florida, offshore
<i>Oregon II</i>	127	06/02-07/13	36788-37059	497-706	Bongo/Neuston	Panama City-Brownsville, shelf
Louisiana	0	06/01-07/30	01-43	454-496	Ring	Louisiana coastline
<i>Hernan Cortez</i>	02	06/07-06/13	A2-A30	731-817	Bongo/Neuston	Northwest Florida, shelf
<i>Jeff and Tina</i>	0003	06/16-07/06	B200-B220	415-447	Bongo/Neuston	East Texas/West Louisiana, shelf
<i>Hernan Cortez</i>	03	06/19-06/22	31-49	818-868	Bongo/Neuston	Southwest Florida, shelf
<i>Western Gulf</i>	15	06/23-06/25	B233-B234	448-453	Bongo	Texas, shelf
<i>Oregon II</i>	130	10/15-11/23	37375-38268	2036-2127	Bongo/Neuston	North-central Gulf

Table 2
Summary of 1983 SEAMAP ichthyoplankton sampling in the northern Gulf of Mexico.

Vessel or state	Cruise	Dates	Station no.	Sample no.	Gear	Location
				2133-2162		
<i>Oregon II</i>	133	03/13-03/29	38604-38775	3339-3351	Bongo/Neuston	East of Mississippi River
<i>Oregon II</i>	134	04/22-05/23	39065-39198	1139-1471	Bongo/Neuston	East-central Gulf, offshore
<i>Oregon II</i>	135	06/01-07/13	39199-39443	1890-2033	Bongo/Neuston	Panama City-Brownsville, shelf
<i>Tommy Munro</i>	135	06/07-06/14	A1-B182	1639-1673	Bongo/Neuston	Mississippi-Alabama, shelf
Louisiana	02	06/13-06/16	01001-07005	1703-1735	Ring	Louisiana coastline
Louisiana	03	06/21-06/23	01001-07005	1736-1765	Ring	Louisiana coastline
<i>Hernan Cortez</i>	01	06/26-06/29	8301-8316	1486-1533	Bongo/Neuston	West-central Florida, shelf
<i>Suncoaster</i>	01	06/29-07/05	B172-B183	1685-1701	Bongo/Neuston	Mississippi-Alabama, shelf
<i>Hernan Cortez</i>	02	07/12-07/19	8317-8335	1534-1590	Bongo/Neuston	Southwest Florida, shelf
<i>Oregon II</i>	138	10/12-10/31	39580-39849	3352-3454	Bongo/Neuston	East of Mississippi River
<i>Tommy Munro</i>	RD83	10/18-10/19	1-3	1884-1889	Bongo	Mississippi, shelf
<i>Oregon II</i>	140	12/08-12/21	40163-40195	1772-1841	Bongo/Neuston	East-central Gulf, offshore

Our research approach for this 2-year project was to (1) thoroughly survey the pertinent literature and compile, consolidate, and synthesize appropriate data for incorporation into bioprofiles of the early life histories of the selected species; and (2) sort, identify, and analyze larval clupeid samples requested from the Southeast Area Monitoring and Assessment Program (SEAMAP), focusing on collections in the northern Gulf during 1982 and 1983 cruises.

Methods and Materials

Ichthyoplankton samples

Samples of larval and early juvenile clupeids from the SEAMAP ichthyoplankton collections were examined for the presence of our target species: *Etrumeus teres*, *Harengula jaguana*, *Opisthonema oglinum*, and *Sardinella aurita*. Samples analyzed in 1982 were from cruises conducted 24 February-17 March (Louisiana, Mississippi, and western Alabama waters only) and 15 April-14 July (Richards et al. 1984), and an additional cruise 15 October-23 November. In 1983, samples were analyzed from cruises conducted 13 March-5 July, and during 12-31 October and 14-21 Decem-

ber (Kelley et al. 1985). For both years our target species were analyzed from station locations throughout the northern Gulf extending south to the limit of the U.S. Exclusive Economic Zone (formerly the FCZ). With the exception of a few localized cruises off Louisiana, Mississippi, and Alabama, stations were generally arranged in a systematic grid at minimum intervals of 55.6 km (30 nautical miles) or one-half degree. SEAMAP vessels were provided by the National Marine Fisheries Service and by state agencies (Tables 1 and 2). Sampling consisted of oblique plankton tows taken with 60-cm bongo nets (0.333-mm mesh) within 5 m of the bottom (at station depths <205 m), or from a depth of 200 m; and 10-min neuston tows with the 1×2-m net (0.947-mm mesh) half submerged (Thompson and Bane 1986). In addition, 0.5-m ring nets with 0.333-mm mesh were used aboard Louisiana and Alabama vessels to take 10-min surface hauls on north-south transects within the 5-m depth contour. Towing speed for all collections was 0.8 m/s. A more detailed treatment of the sampling grid and procedures is presented elsewhere (Stuntz et al. 1982, Thompson and Bane 1986).

Table 3

Number of SEAMAP stations sampled for clupeid larvae gulfwide, 1982 and 1983. No samples taken in January, August, or September.
NS = no samples taken.

Year	Gear and depth	Feb	Mar	Apr	May	June	July	Oct	Nov	Dec
Bongo										
1982	<40 m	7	33			52	10		11	
	40–182 m		43	5	11	36	8		13	
	>182 m		1	64	60	14	8	3	5	
	Total	7	77	69	71	102	26	3	29	NS
1983	<40 m		3		4	27	17	18		
	40–182 m		4	5	5	25	21	9		3
	>182 m		8	22	75	3	6	12		21
	Total	NS	15	27	84	55	44	39	NS	24
Neuston or Ring										
1982	<40 m					70	30			
	40–182 m			5	11	36	7		1	
	>182 m			63	62	14	8	8	2	
	Total	NS	NS	68	73	120	45	8	3	NS
1983	<40 m				4	65	15			
	40–182 m		3	5	5	22	21	3		3
	>182 m		10	22	73	1	6	22		20
	Total	NS	13	27	82	88	42	25	NS	23

Clupeid larvae were identified to the lowest taxonomic level possible and verified against available ichthyoplankton reference collections. Specimens of *O. oglinum* and *S. aurita* that had not yet developed most of their dorsal and anal fin rays, ~16 mm standard length (SL), were often difficult to distinguish, though pigmentation differences allowed us to separate most individuals larger than 8 mm SL. *Opisthonema oglinum* and *S. aurita* were grouped into an *Opisthonema/Sardinella* complex when positive identifications to species could not be made. Only clupeids of the four target species plus gulf menhaden were found in the samples.

Target species were enumerated and measured. Lengths were measured to the nearest tenth millimeter and are presented in 1-mm increments (i.e., 1.0–1.9 mm, 2.0–2.9 mm) in the length-frequency histograms. Standard length was considered synonymous with notochord length in preflexion larvae. Any fishes larger than 25.9 mm SL were considered juveniles and not included in this analysis. In each sample, all fish of a target species or species group (i.e., *Opisthonema/Sardinella*) were measured unless there were more than 52 individuals. For collections of over 52 specimens, we measured the longest and shortest individuals and used a random-numbers table to select 50 others from a dish with a grid system. We adjusted the length-frequency histograms from net collections with greater than 52 larvae of a given species by a multiplier to give equal weight to the length data subsampled from the larger collections.

Spawning season and location (depth or distance from shore), larval distribution and abundance, and larval ecology (i.e., temperature and salinity at time of capture) were determined for all target species. Yearly abundance of each larval species was determined at three depth zones: inner shelf

(depths <40 m), outer shelf (40–182 m), and offshore (>182 m). Length-frequency data and station abundances for each species or species group were plotted by gear type and month. Monthly groupings were considered optimal because they allowed variation in the sampling effort (cruise tracks) and spawning intensity or site location to be viewed over time without considerable loss of sample size or geographic coverage. Abundances of larvae caught in unmetered neuston or 0.5-m ring nets are listed as catch-per-unit-effort (CPUE), where a unit of effort is defined as one complete tow (~10 min). Only bongo nets were metered, allowing calculations of the volume of water filtered. Abundances of fish captured in bongo nets are presented as the number of larvae under 10 m² of sea surface, which is written in the text as no. fish/10 m². Yearly mean abundances were calculated over those months when capture of a species was deemed likely, referred to as the larval season. Both positive and zero-catch stations were included in mean abundance estimates. The number of total stations sampled each month is given in Table 3.

Bioprofiles

We found much of the literature reviewed in the bioprofiles (see Appendix) through computer-assisted literature searches utilizing on-line databases such as *Aquatic Science Abstracts* (1978–83), *BIOSIS* (1969–83), *Comprehensive Dissertation Abstracts* (1861–1983), *Oceanic Abstracts* (1964–83), and *Zoological Record* (1978–80).

The total number of literature citations on these species is somewhat deceptive; review of the literature reveals that relatively few early-life-history studies from the Gulf of Mexico have targeted these species, except a number of studies along the west coast of Florida. The available summary information often pieced together data from throughout the world's oceans or on similar species of the same genus. For these reasons, we have purposely avoided using summations of all the available information to make all-inclusive statements on spawning seasonalities, egg and larval distributions, meristics, etc., in our early-life-history bioprofiles. We have instead reported specific facts from specific authors and locales so that readers can locate information relevant to their particular problems or decide how much weight to give to each finding based on its timeliness or proximity to a given geographical area. In the absence of data from the Gulf or on the appropriate species, we have provided information from other areas, oceans, or species, and have so indicated in each instance.

Results

Etrumeus teres

Round herring larvae were found mostly on the continental shelf across the Gulf, except off southern Texas where sampling coverage during the spawning season of this species was poor (Figs. 1–4). Offshore (depths >182 m), larvae were less abundant but were again found across the Gulf. Over the 2-year period, 2962 *E. teres* larvae were collected.

High concentrations of round herring larvae were found on the outer shelf (depths 40–182 m) during sampling near the Mississippi River delta region in 1982. Mean abundance on the outer shelf in both 1982 and 1983 was greater than that of the other target clupeids (Table 4). When sampling was primarily offshore, most larvae were captured near the shelf break, again indicating potential concentrations on the outer shelf. Abundance appeared to be relatively low on the inner shelf (depths <40 m), which may be a reflection of poor coverage of the inner-shelf stations during February–May, especially in 1983, and the extensive inner-shelf coverage during June when larvae were less likely to be found.

Larvae were collected late February–early June (Table 5). This was the only target clupeid collected February–March. The majority of *E. teres* larvae were taken March–April, but a few large catches were recorded in May. No *E. teres* larvae were collected from the October–December sampling. Though no SEAMAP samples were taken in January, length-frequency distributions from collections in February and early March indicate that spawning probably occurred in at least late January (Figs. 5–8). Larvae in the size range 3–5 mm SL dominated February, March, and April bongo collections. A progression towards larger larvae occurred in May.

Surface temperatures and salinities at locations where recently hatched larvae (<4.0 mm SL) were captured were 16.7°–23.8°C and 33.8–36.5 ppt (Table 6). For all sizes of larvae collected, temperature ranges were 15.0°–30.0°C and salinities 28.7–37.5 ppt. Mean values were 24.5°C and 36.2 ppt for 1982 (salinity means for April–June stations only), and 21.0°C and 35.5 ppt for 1983.

Harengula jaguana

Scaled sardine larvae were found virtually everywhere inner-shelf stations were sampled (Figs. 9–12). High abundances of larvae were consistently found at stations along the coasts of Mississippi–Alabama, the eastern third of Texas, and western Louisiana. In June 1982, scaled sardine larvae were abundant on the west Florida shelf as well. Coverage of the south Texas shelf was poor, but the few samples taken there in July revealed relatively high abundances. On the outer shelf, abundances were much lower (Table 4), but larvae were occasionally taken in those waters at abundances greater than 10 fish/10 m². Larvae were virtually absent from offshore waters (depths >182 m), but offshore station coverage was poor during the summertime peak spawning period of this species.

Over the 2-year period, 4295 *H. jaguana* larvae were collected. Both years, *H. jaguana* ranked lowest in overall mean abundance among the four target clupeids (Table 4). At inner-shelf stations, however, they were the most commonly encountered clupeid larvae and were captured at 25% of bongo stations sampled.

Harengula jaguana larvae were collected late April–mid July (Table 7), with all but 11 larvae collected during June and July inner-shelf sampling. Recently hatched larvae (1.9–3.9 mm) taken in June and July were all found inshore of the 51-m depth contour, and many were collected inshore of 10 m. There was some indication of modal progression toward larger larvae from June to July in 1982 surface-gear collections (neuston and half-meter ring nets), but in general no clear progression was evident (Figs. 13–16). Larvae taken in April and May from offshore stations were usually captured as lone individuals and most often in the neuston net.

Surface temperatures and salinities at locations where recently hatched larvae (<4.0 mm SL) were captured were 25.2°–32.0°C and 10.4–36.4 ppt (Table 6). Temperature and salinity ranges for all sizes of larvae collected were 20.0°–32.0°C and 10.4–37.3 ppt. Mean values were 28.7°C and 31.8 ppt for 1982, and 27.4°C and 26.3 ppt for 1983.

Two-thirds of the *H. jaguana* larvae taken were from surface collections; however, surface tows had a percentage of positive catches (12%) similar to that of oblique bongo tows (Table 7).

ETRUMEUS TERES

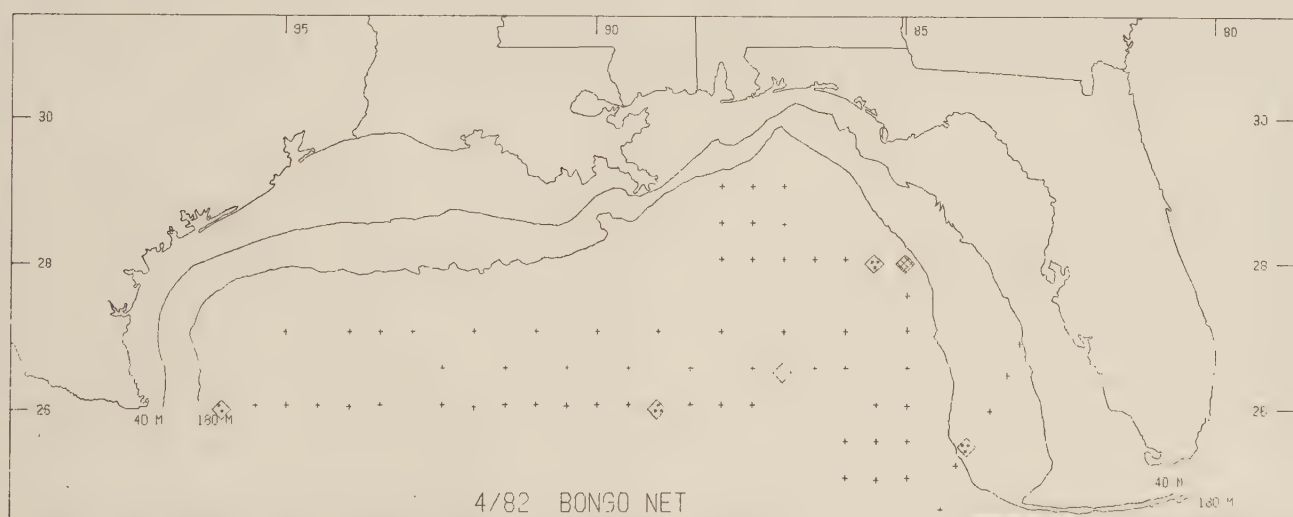
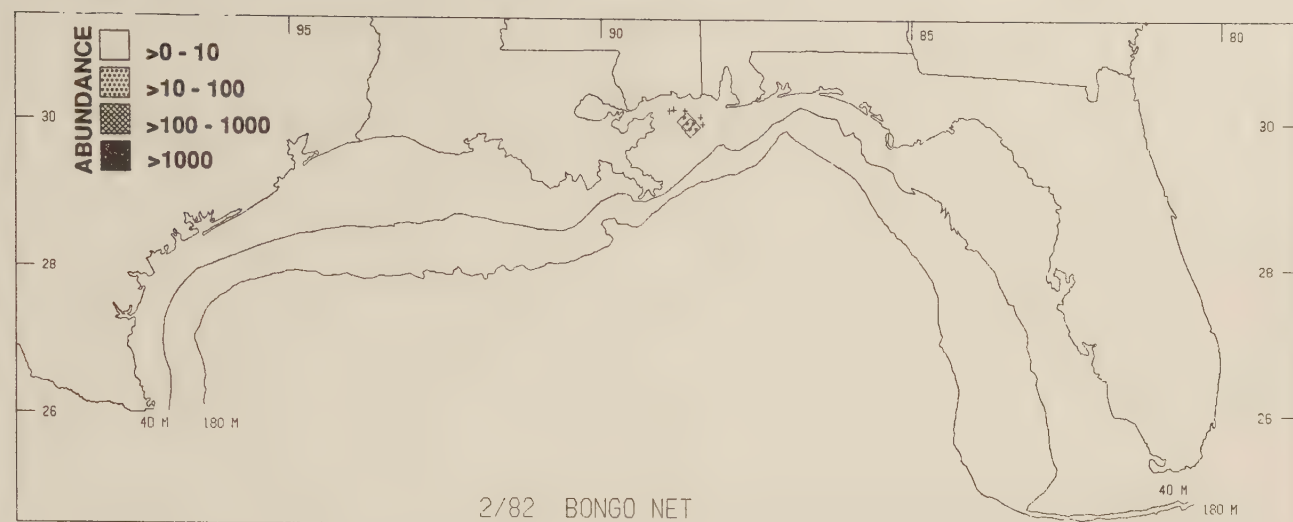


Figure 1
Distribution and abundance ($N/10 \text{ m}^2$) of *Etrumeus teres* larvae for positive-catch months during 1982 SEAMAP bongo net collections. Stations sampled (+).

ETRUMEUS TERES

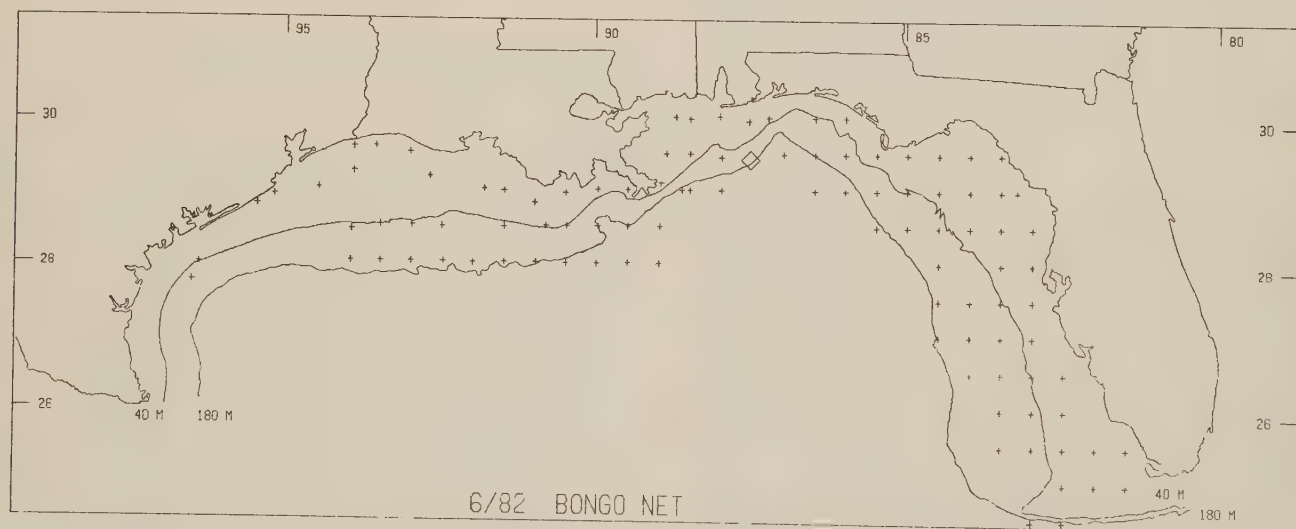
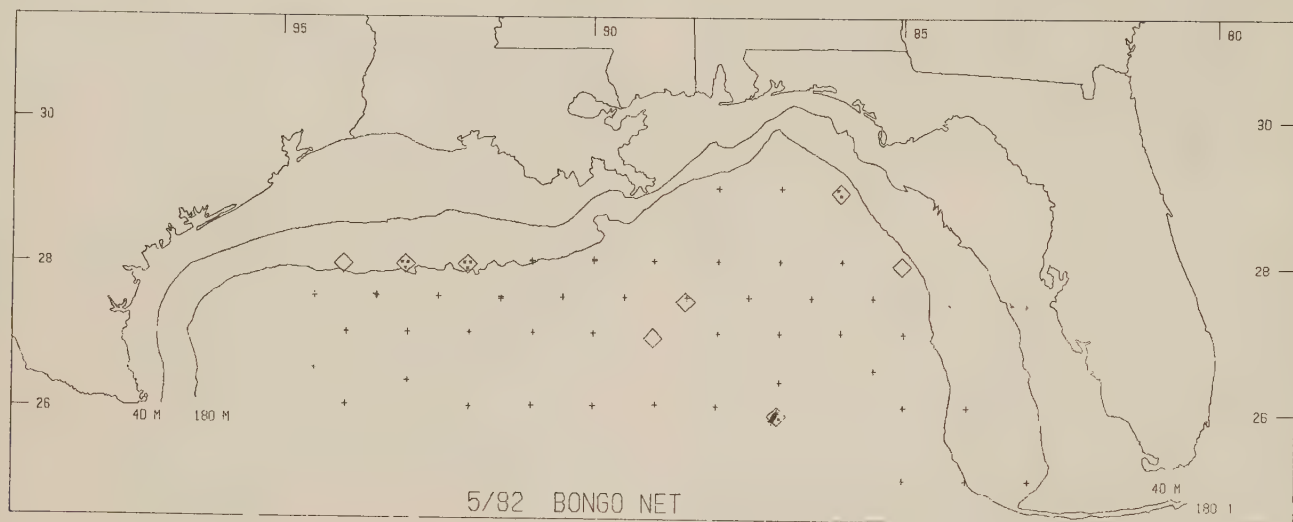


Figure 1 (continued)

ETRUMEUS TERES

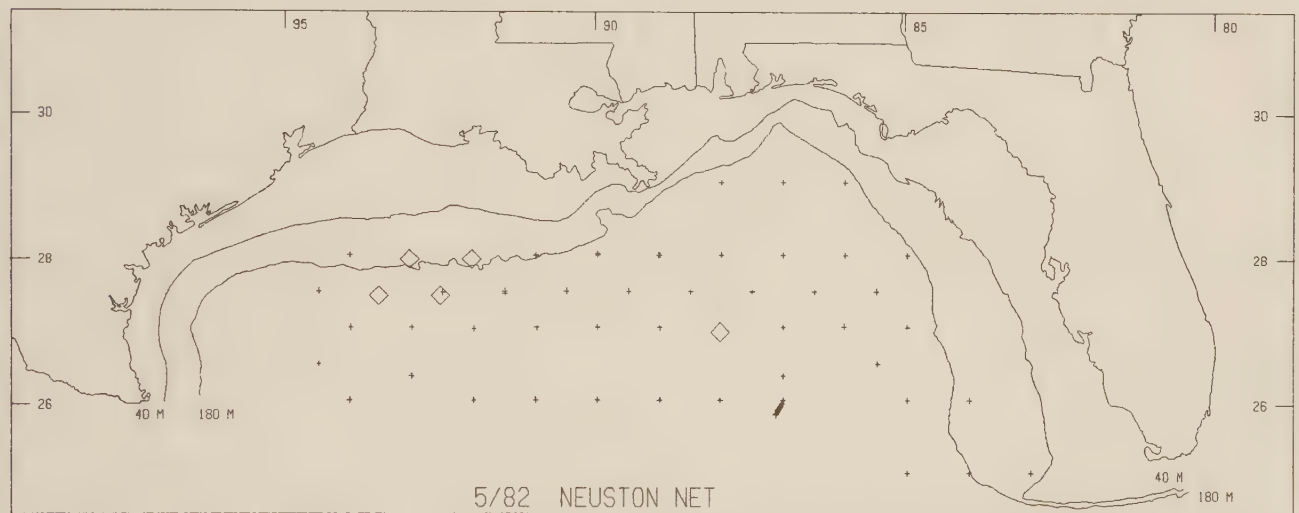
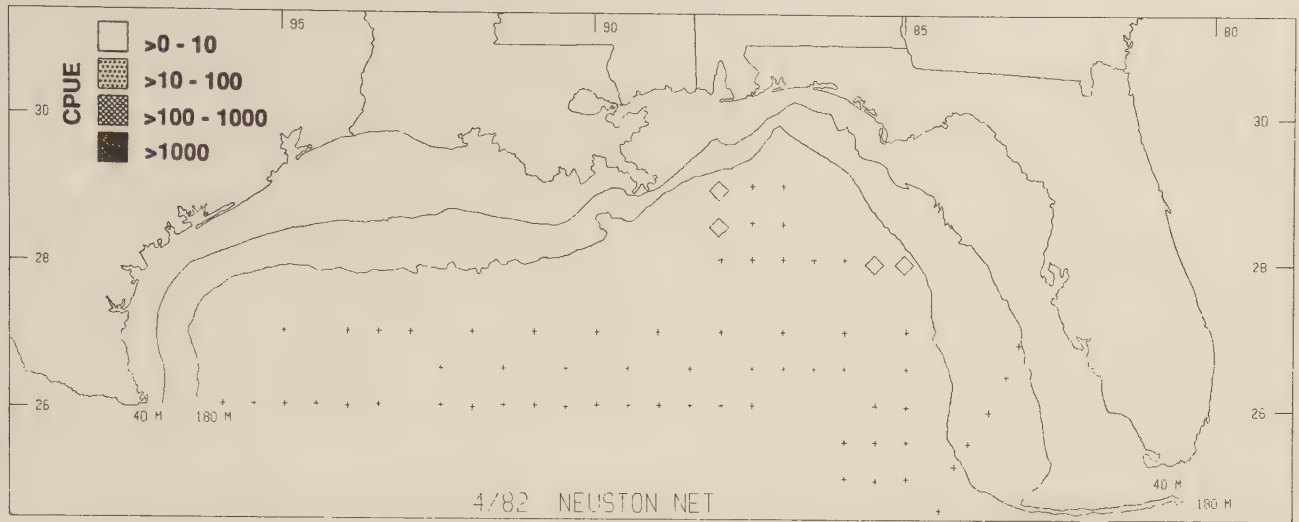


Figure 2

Distribution and CPUE (N/tow) of *Etrumeus teres* larvae for positive-catch months during 1982 SEAMAP neuston net collections. Stations sampled (+).

ETRUMEUS TERES

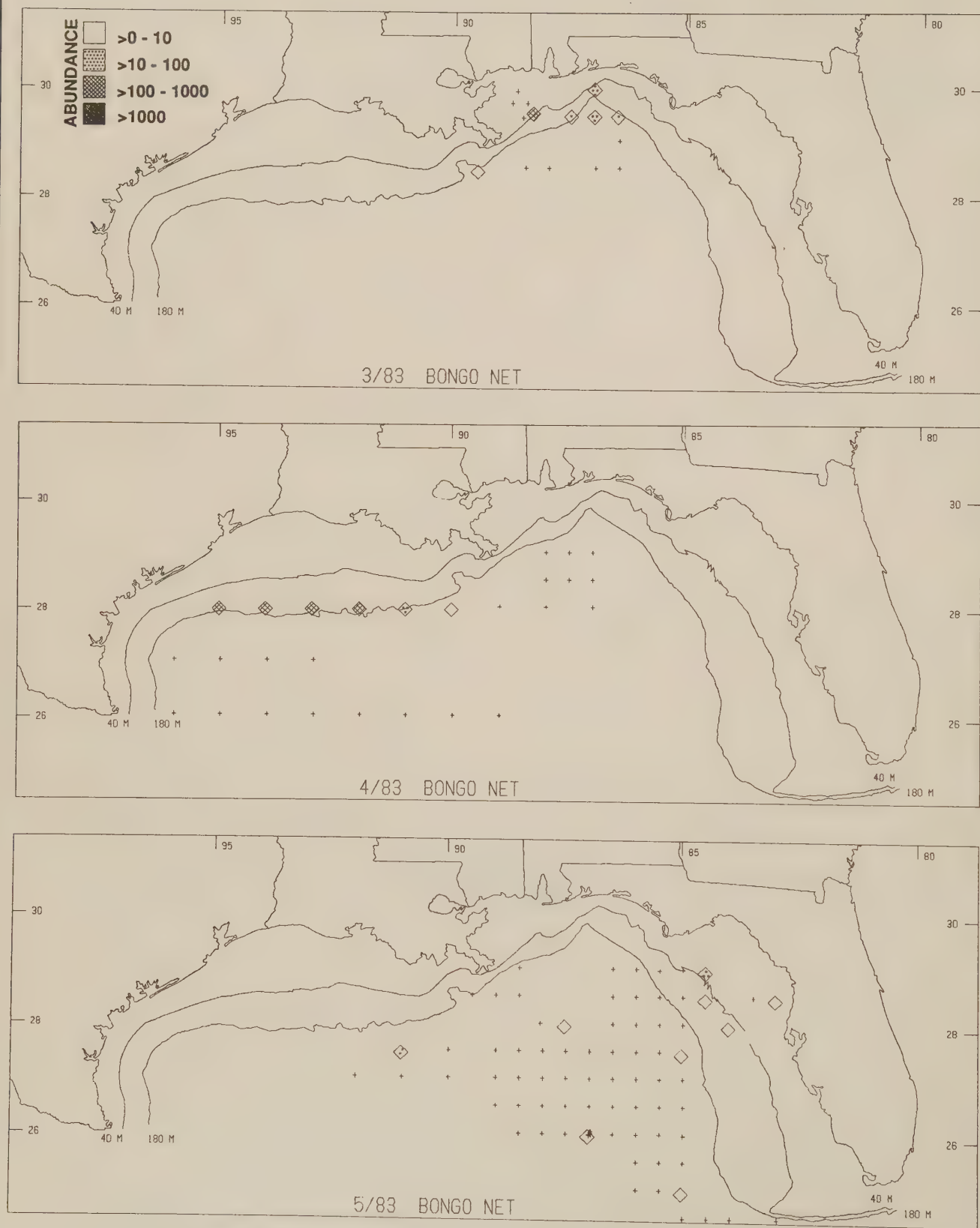


Figure 3

Distribution and abundance (N/10 m²) of *Etrumeus teres* larvae for positive-catch months during 1983 SEAMAP bongo net collections. Stations sampled (+).

ETRUMEUS TERES

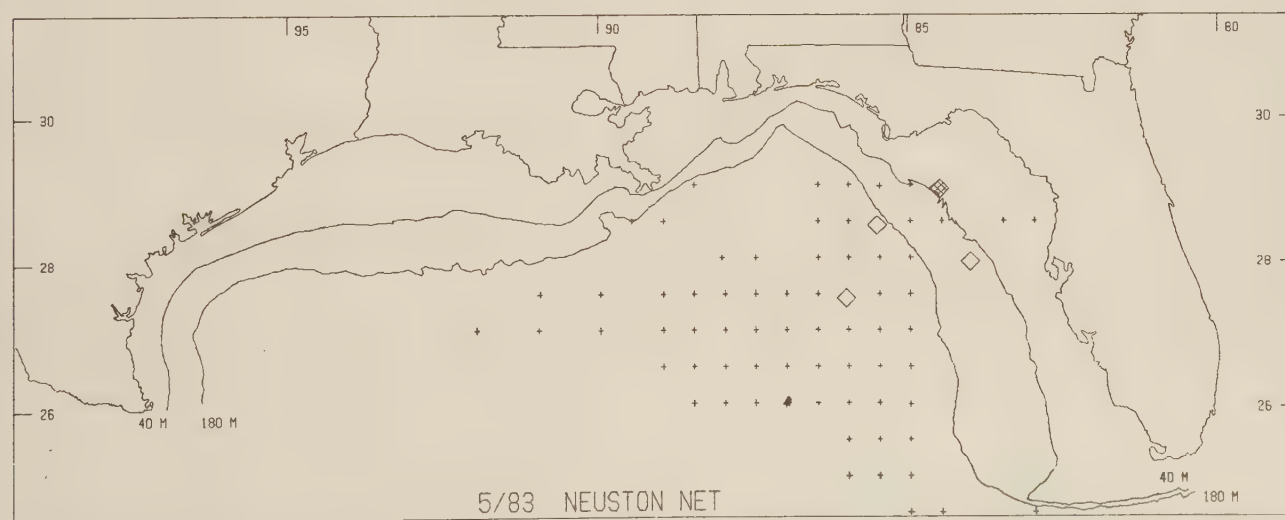
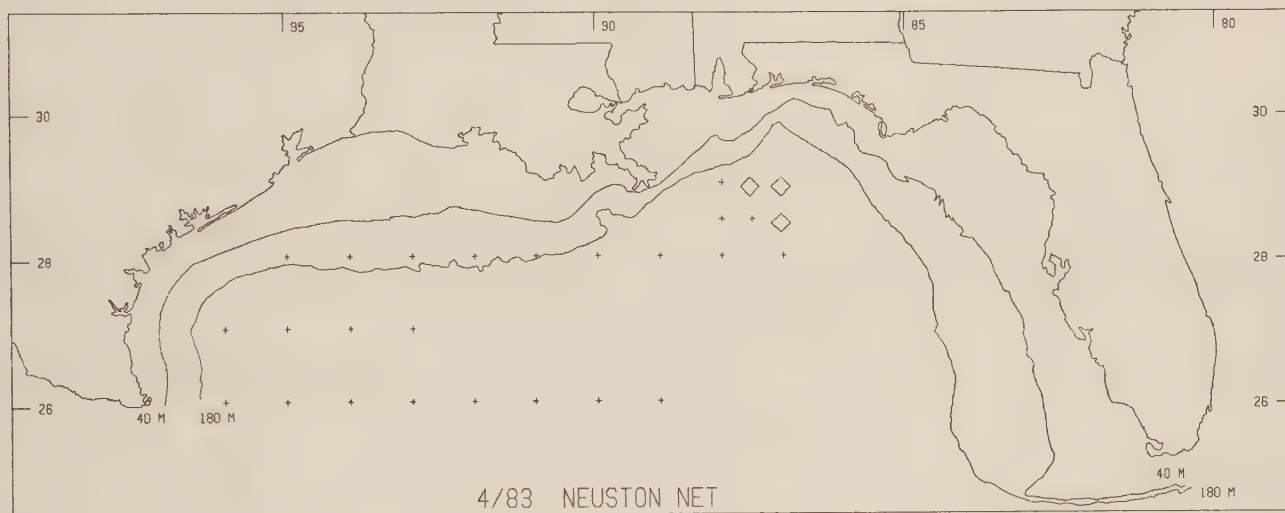
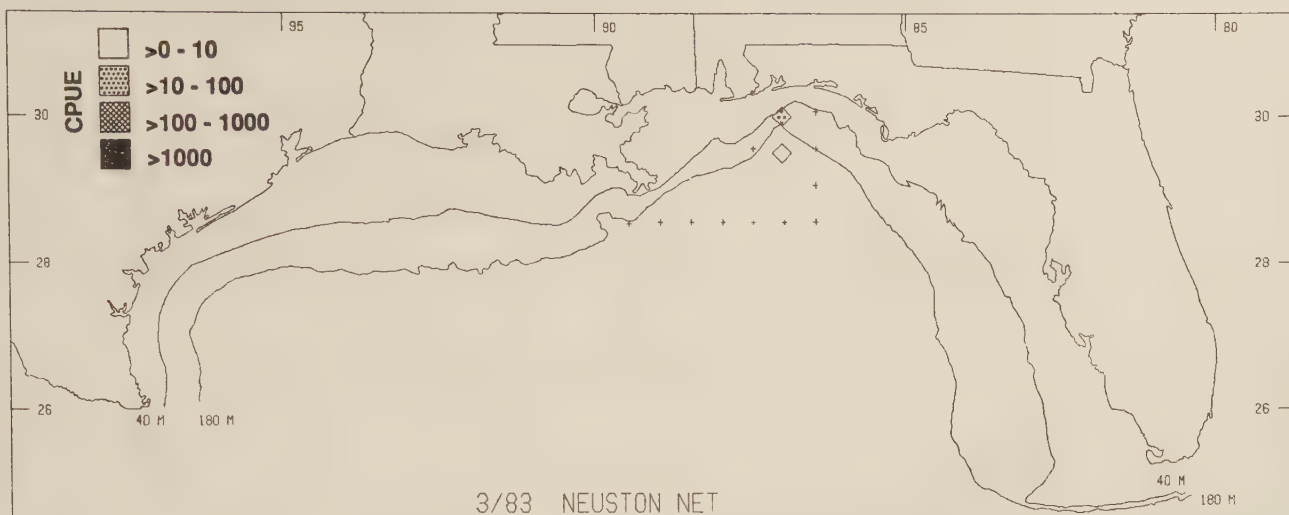


Figure 4

Distribution and CPUE (N/tow) of *Etrumeus teres* larvae for positive-catch months during 1983 SEAMAP neuston net collections. Stations sampled (+).

Table 4			
Abundance ($N/10\text{ m}^2$) and depth distribution of target clupeid larvae by species (or generic complex) and year. Numbers in parentheses are positive-catch bongo stations per total stations sampled. Abundances and total stations are for months during reported larval season.			
Taxa	<40 m	40–182 m	>182 m
<i>Etrumeus teres</i>			
1982	12.7 (14/103)	45.5 (37/108)	2.9 (10/144)
1983	0.9 (3/34)	35.0 (9/42)	1.5 (9/129)
<i>Harengula jaguana</i>			
1982	20.4 (29/106)	1.6 (7/116)	0.1 (2/155)
1983	9.4 (14/69)	0.4 (2/69)	0.1 (2/126)
<i>Opisthonema oglinum</i>			
1982	67.4 (24/106)	1.9 (2/116)	0.0 (0/155)
1983	11.0 (13/69)	0.1 (2/69)	0.0 (0/126)
<i>Sardinella aurita</i>			
1982	27.0 (22/106)	21.5 (11/116)	3.4 (5/155)
1983	56.8 (14/69)	3.4 (5/69)	<0.1 (1/126)
<i>Opisthonema/Sardinella</i> complex			
1982	67.6 (15/106)	2.2 (2/116)	0.0 (0/155)
1983	4.7 (8/69)	0.0 (0/69)	0.0 (0/126)

Table 5					
<i>Etrumeus teres</i> mean larval abundance ($N/10\text{ m}^2$) as determined from metered bongo tows, and mean catch-per-unit-effort (number captured/tow) as determined from neuston and unmetered 0.5-m ring net tows for positive-catch stations only. Spawning season considered to be October–June (Ditty et al. 1988; this work). For total SEAMAP yearly sampling effort by month, gear type, and depth, see Table 3. NS = no samples taken; NA = data not available.					
Mean variable	February	March	April	May	June
Bongo catch					
1982	12.5 ¹ (2/7)	115.3 (45/77)	5.7 (6/69)	3.6 (10/71)	<0.1 (1/102)
1983	NS	34.8 (6/15)	55.8 (6/27)	1.6 (9/84)	0.0 (0/55)
Neuston or ring catch					
1982	NS	NS	1.8 (4/68)	2.3 (6/73)	0.0 (0/120)
1983	NS	13.5 (2/13)	3.3 (3/27)	176.0 (4/82)	0.0 (0/88)
Surface salinity (ppt)					
1982	NA	NA	35.6 (33–37)	36.9 (36–38)	30.3
1983		34.8 (29–36)	34.7 (32–36)	36.4 (35–37)	
Surface temperature (°C)					
1982	17.0	19.4 (15–23)	23.9 (22–27)	24.4 (23–27)	30.0
1983		18.0 (17–19)	20.8 (19–22)	23.0 (21–26)	
Station depth (m) ²					
1982	18.5 ³ (11–26)	51.6 (13–88)	1279 (115–3203)	813 (71–3148)	71
1983		193 (46–440)	454 (79–1463)	1113 (29–3347)	

¹Frequency of occurrence: number of positive-catch stations over number of stations sampled.

²Sampling methodology for bongo nets limits tows to upper 200 m of water (see Methods section).

³Range of values.

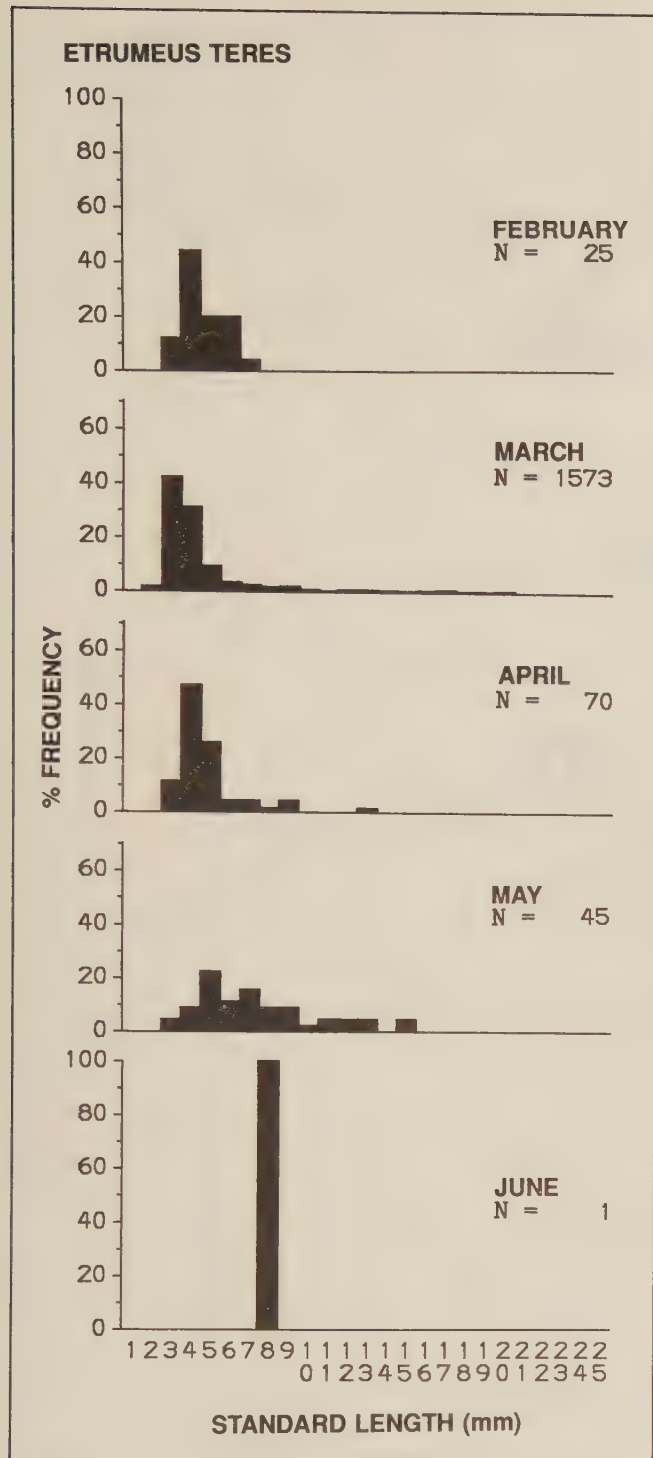


Figure 5

Monthly size-frequency distribution of *Etrumeus teres* larvae for positive-catch months during 1982 SEAMAP bongo net collections. *N* = total number caught.

Figure 7

Monthly size-frequency distribution of *Etrumeus teres* larvae for positive-catch months during 1983 SEAMAP bongo net collections. *N* = total number caught.

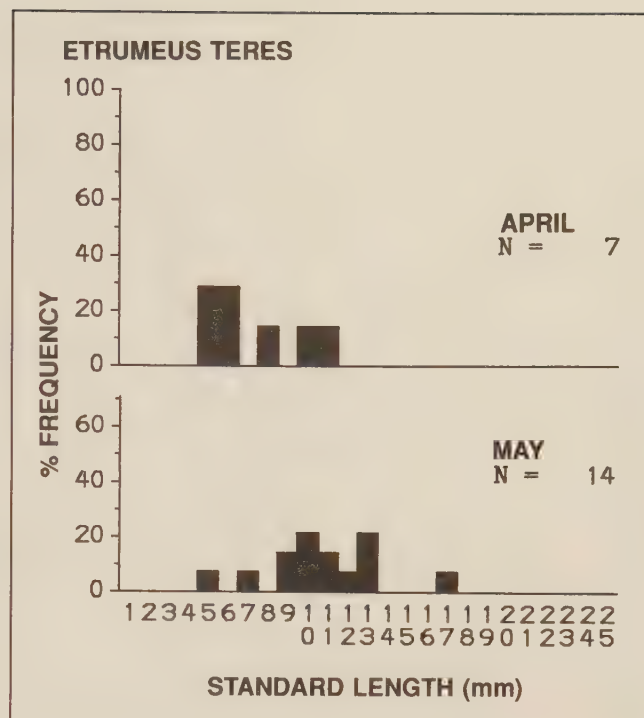
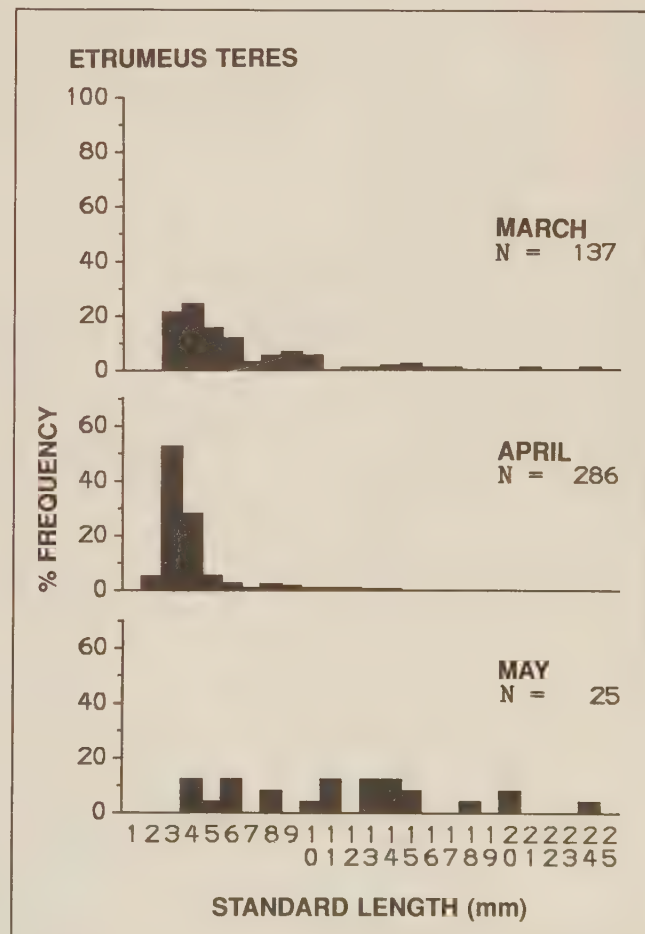


Figure 6

Monthly size-frequency distribution of *Etrumeus teres* larvae for positive-catch months during 1982 SEAMAP neuston net collections. *N* = total number caught.



HARENGULA JAGUANA

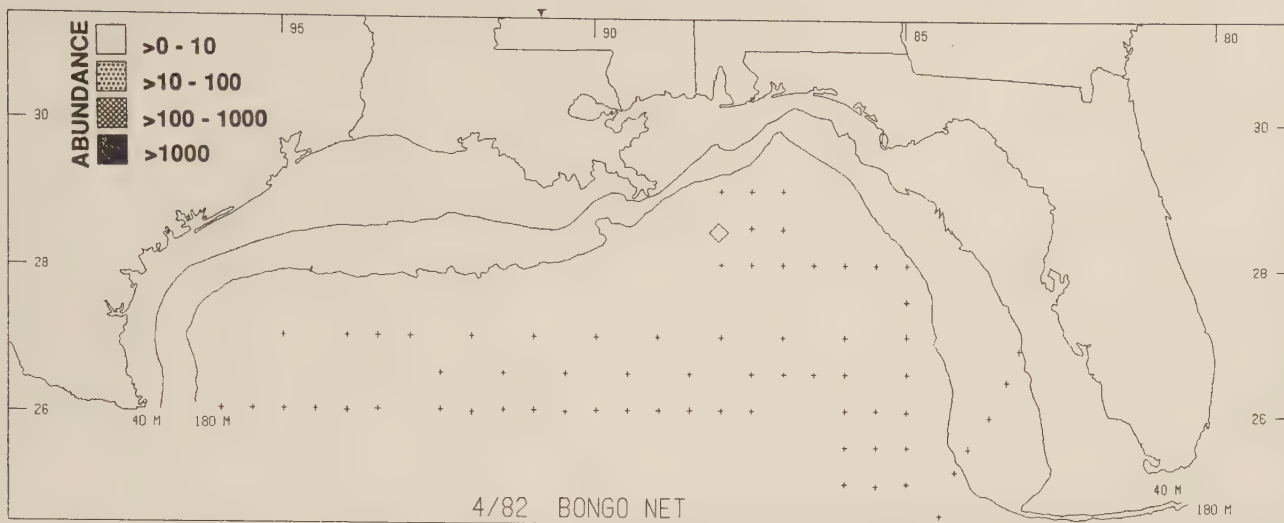


Figure 9
Distribution and abundance ($N/10 \text{ m}^2$) of *Harengula jaguana* larvae for positive-catch months during 1982 SEAMAP bongo net collections. Stations sampled (+).

HARENGULA JAGUANA

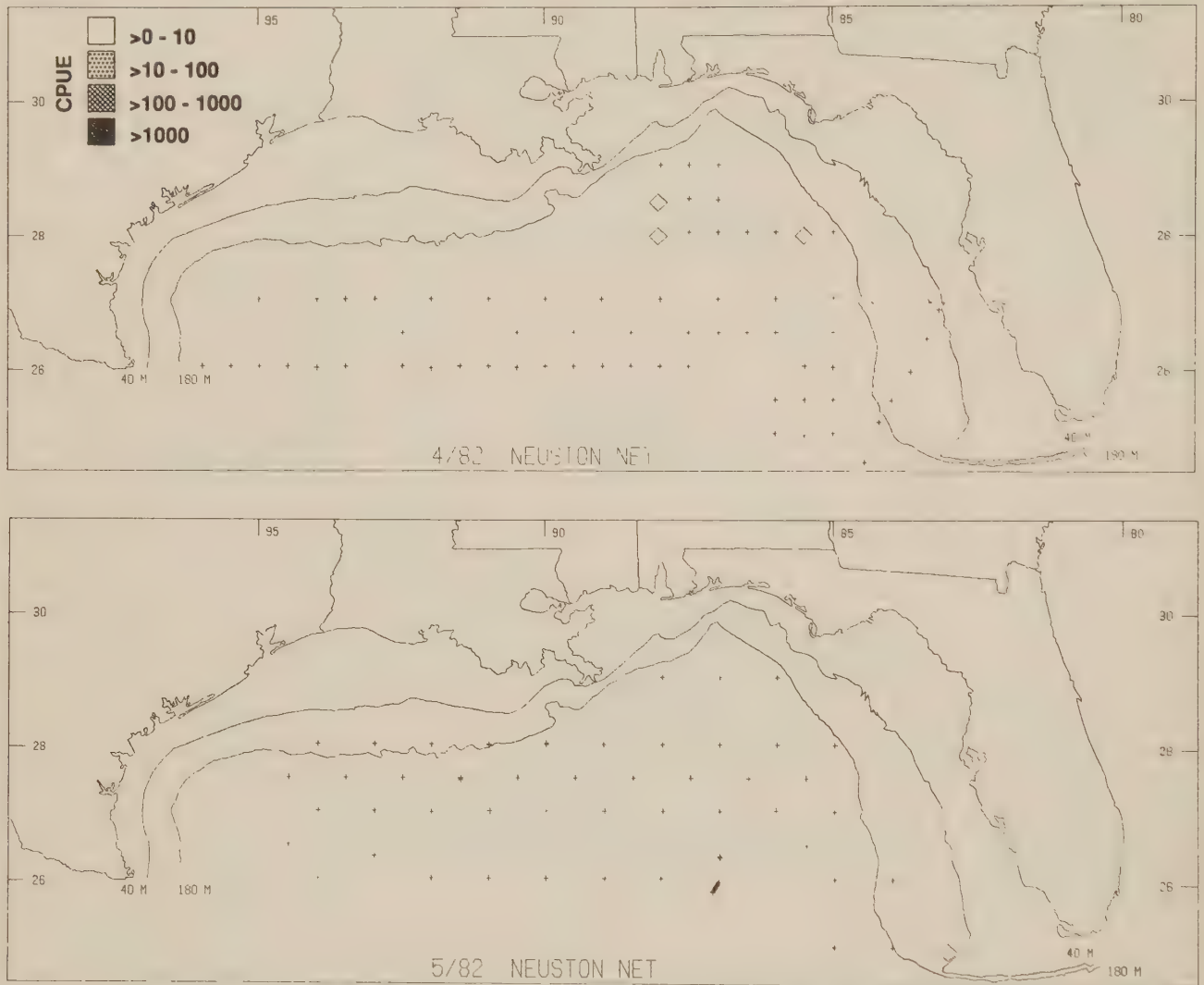


Figure 10

Distribution and CPUE (N/tow) of *Harengula jaguana* larvae for positive-catch months during 1982 SEAMAP neuston and half-meter ring net collections. Stations sampled: + neuston, * ring nets.

HARENGULA JAGUANA

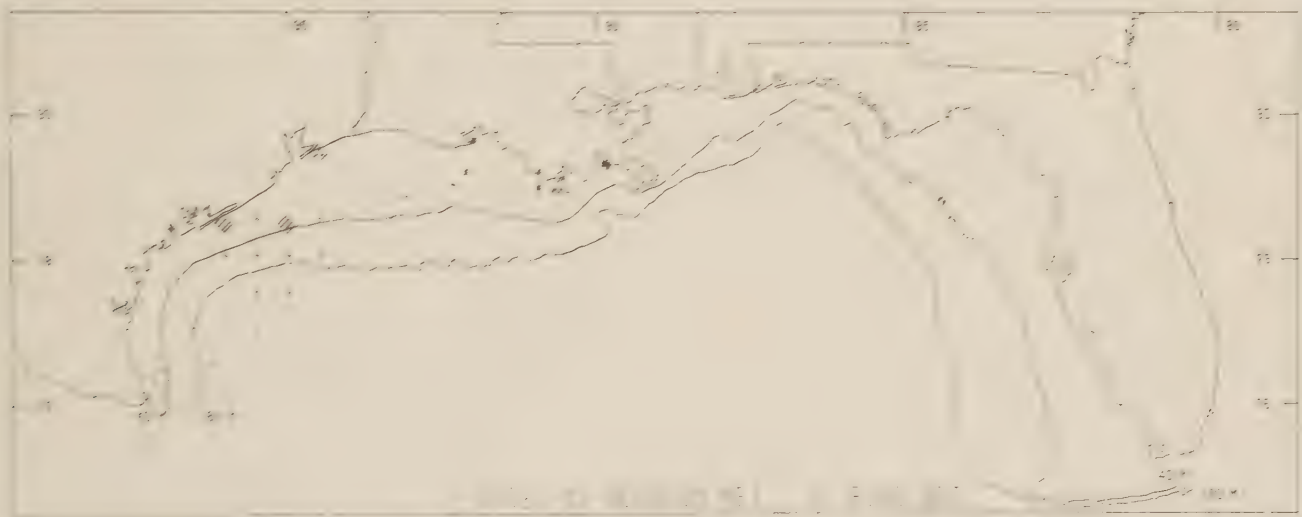
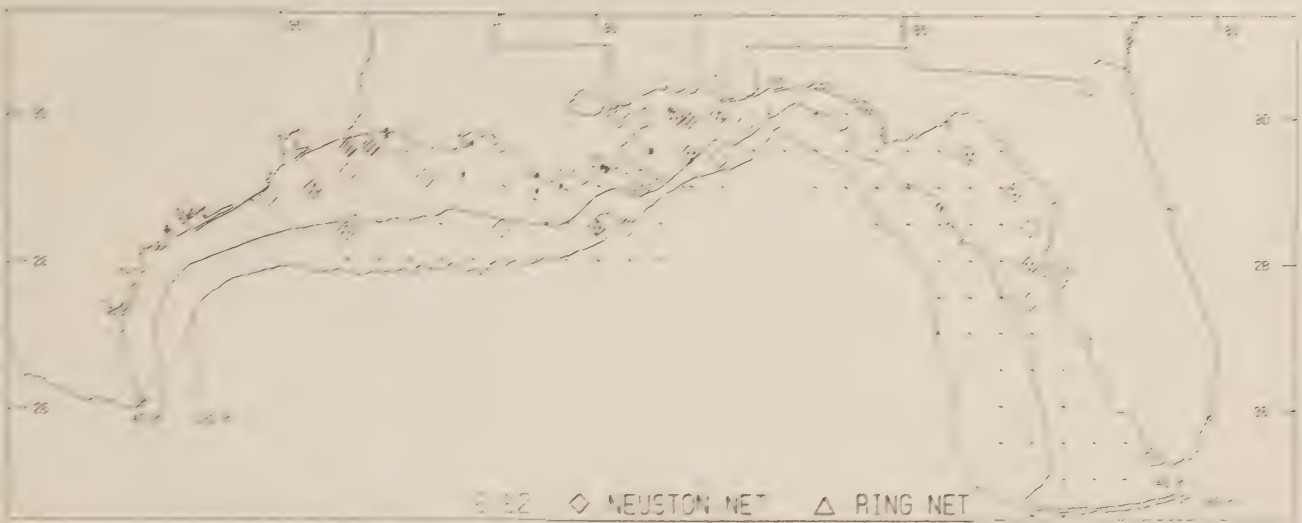


Figure 10 (continued)

HARENGULA JAGUANA

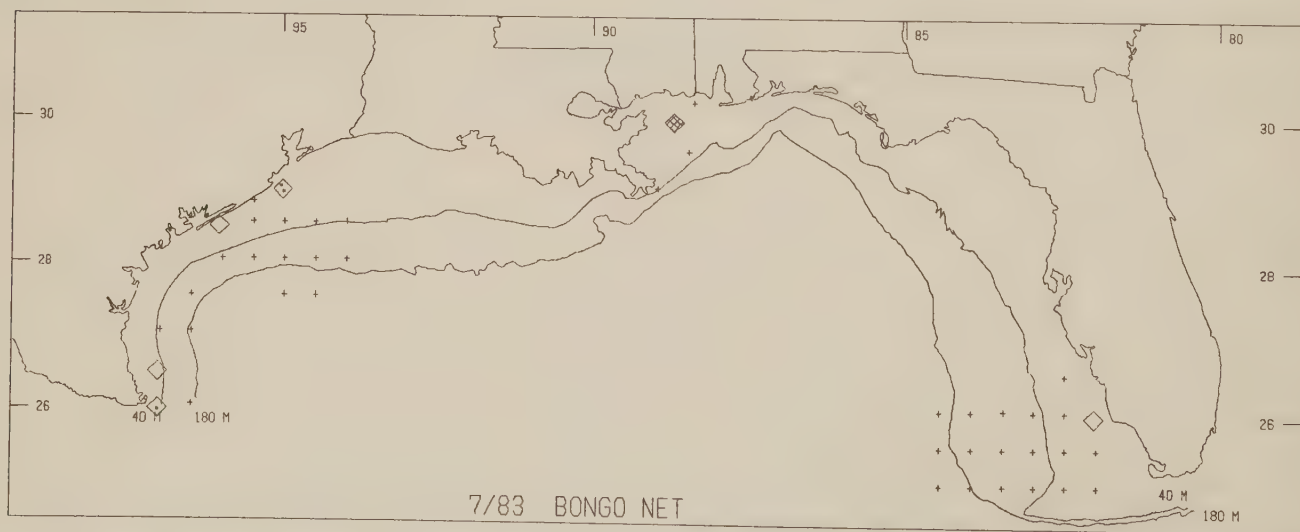
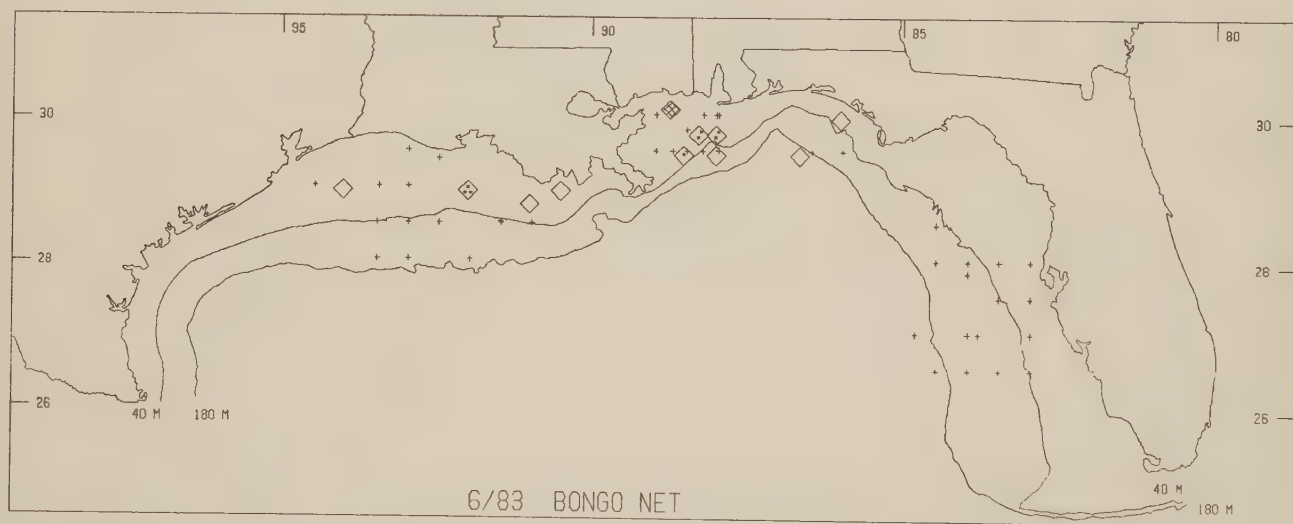
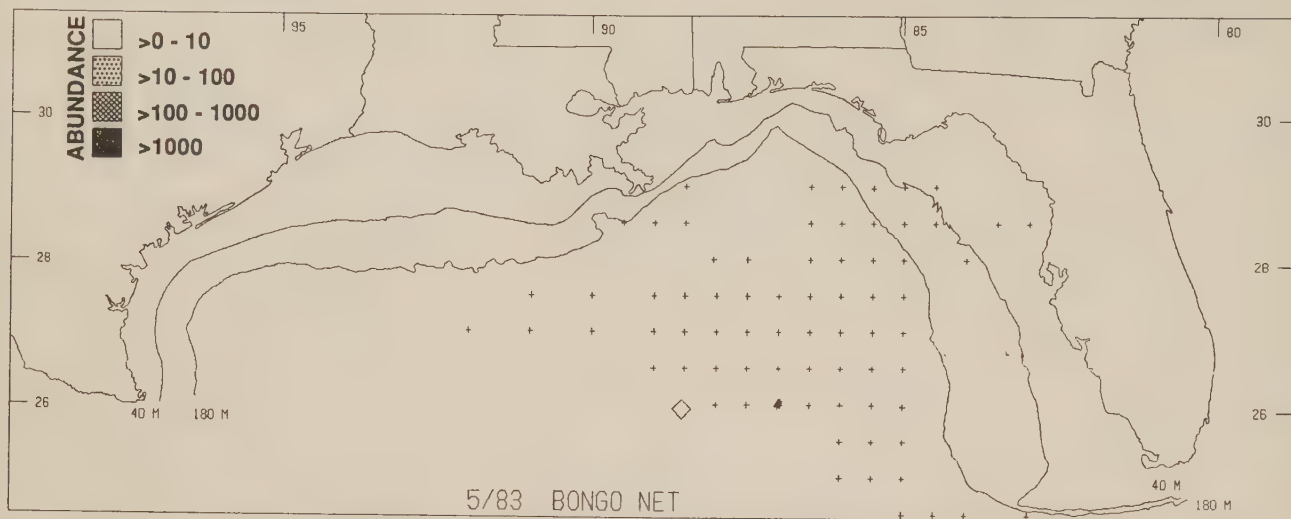


Figure 11

Distribution and abundance ($N/10\text{ m}^2$) of *Harengula jaguana* larvae for positive-catch months during 1983 SEAMAP bongo net collections. Stations sampled (+).

HARENGULA JAGUANA

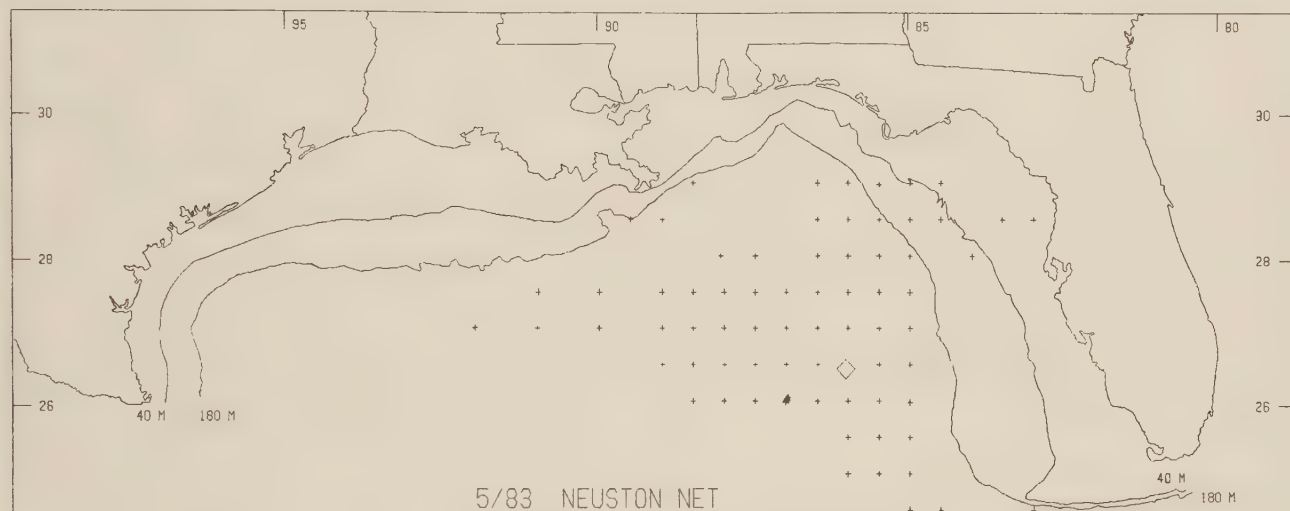
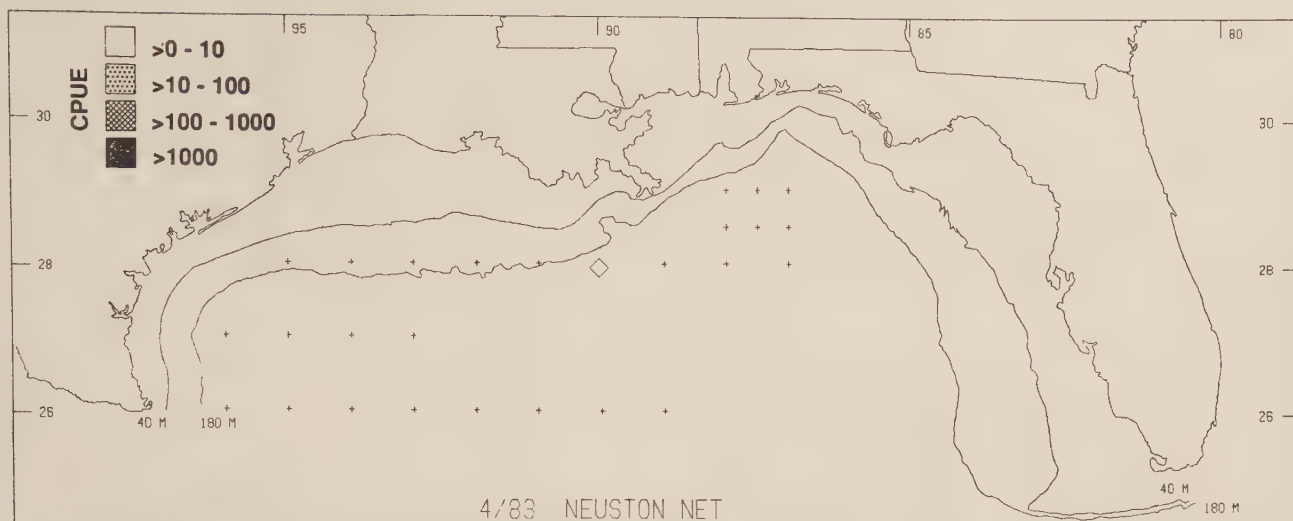


Figure 12

Distribution and CPUE (N/tow) of *Harengula jaguana* larvae for positive-catch months during 1983 SEAMAP neuston and half-meter ring net collections. Stations sampled: + neuston, * ring nets.

HARENGULA JAGUANA

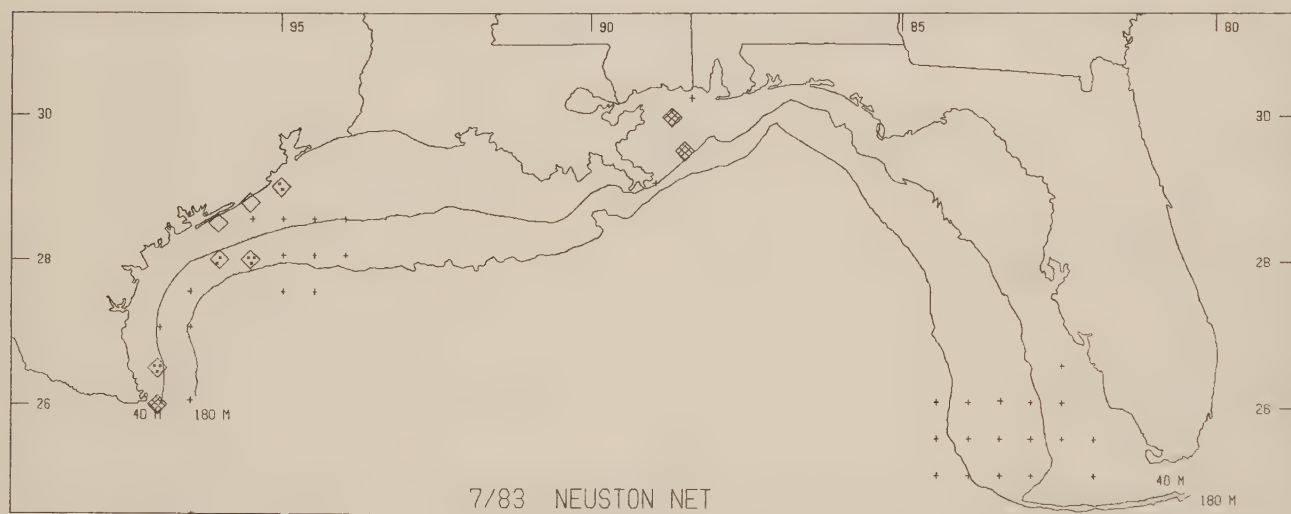
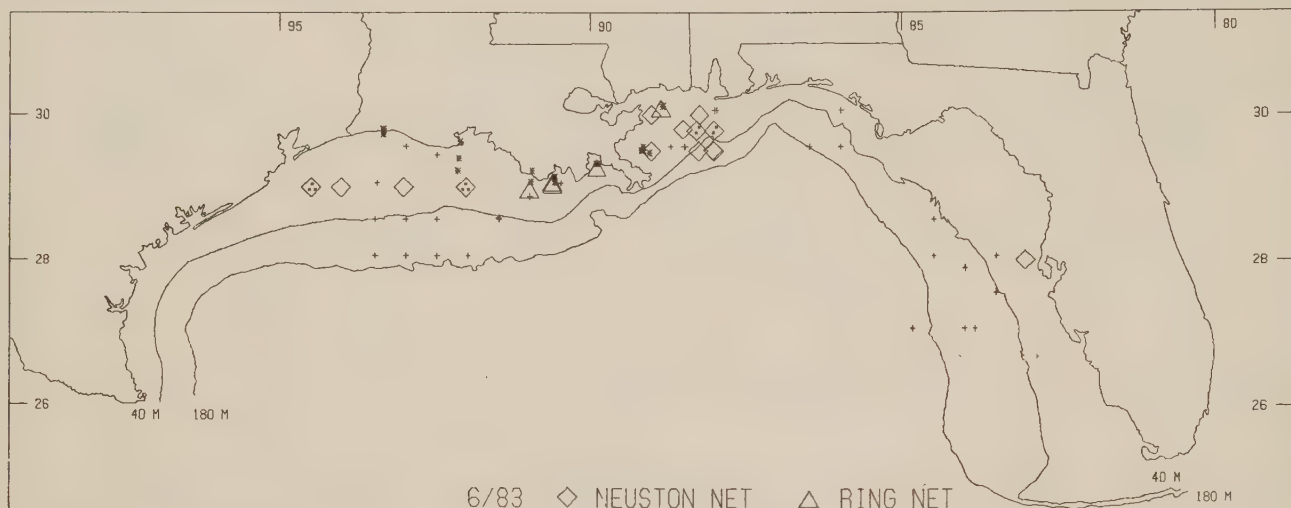


Figure 12 (continued)

Table 7

Harengula jaguana mean larval abundance ($N/10\text{ m}^2$) as determined from metered bongo tows, and mean catch-per-unit-effort (number captured/tow) as determined from neuston and unmetered 0.5-m ring net tows for positive-catch stations only. Spawning season considered to be January–November (Ditty et al. 1988; this work). For total SEAMAP yearly sampling effort by month, gear type, and depth groupings, see Table 3.

Mean variable	Year	April	May	June	July
Bongo catch	1982	<0.1 ¹ (1/69)	0.0 (0/71)	26.3 (30/102)	37.9 (7/26)
	1983	0.0 (0/27)	<0.1 (1/84)	8.3 (11/55)	15.9 (6/44)
Neuston or ring catch	1982	1.0 (3/68)	3.0 (1/73)	42.1 (22/120)	84.8 (6/45)
	1983	1.0 (1/27)	1.0 (1/82)	11.1 (20/88)	136.9 (9/42)
Surface salinity (ppt)	1982	36.8	36.5	31.1 (10–37)	33.8 (18–36)
	1983	32.0	37.0	24.0 (12–35)	27.4 (15–35)
Surface temperature (°C)	1982	24.2 ² (23–25)	25.7	29.1 (27–32)	29.4 (27–32)
	1983	20.0	27.2 (27–28)	26.8 (25–30)	28.6 (21–30)
Station depth (m) ³	1982	1894 (567–2434)	52	52 (6–840)	26 (9–58)
	1983	541	3155 (3018–3292)	35 (5–395)	26 (9–53)

¹Frequency of occurrence: number of positive-catch stations over number of stations sampled.

²Range of values.

³Sampling methodology for bongo nets limits tows to upper 200 m of water (see Methods section).

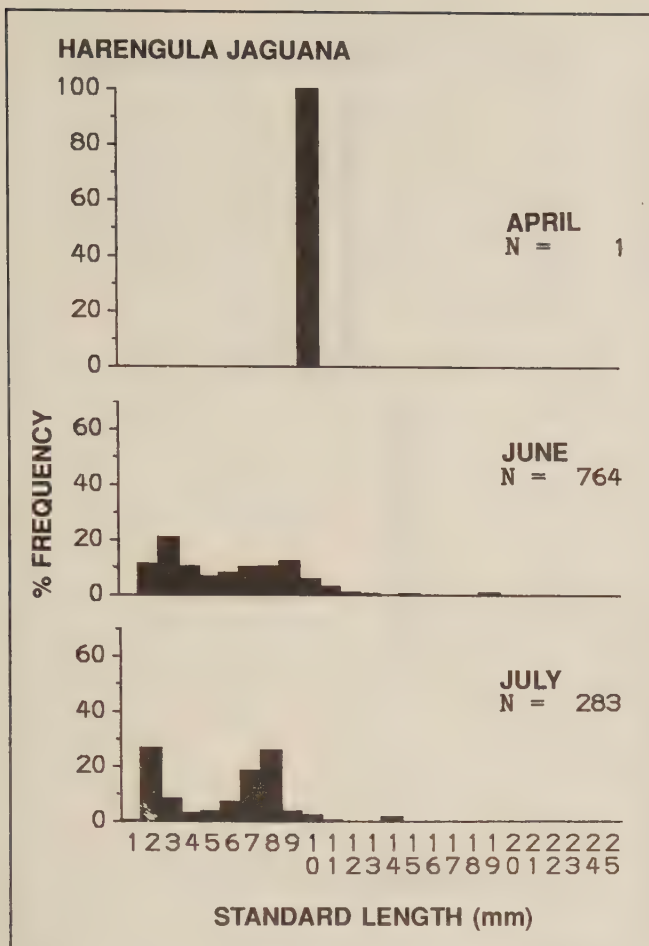


Figure 13

Monthly size-frequency distribution of *Harengula jaguana* larvae for positive-catch months during 1982 SEAMAP bongo net collections. *N* = total number caught.

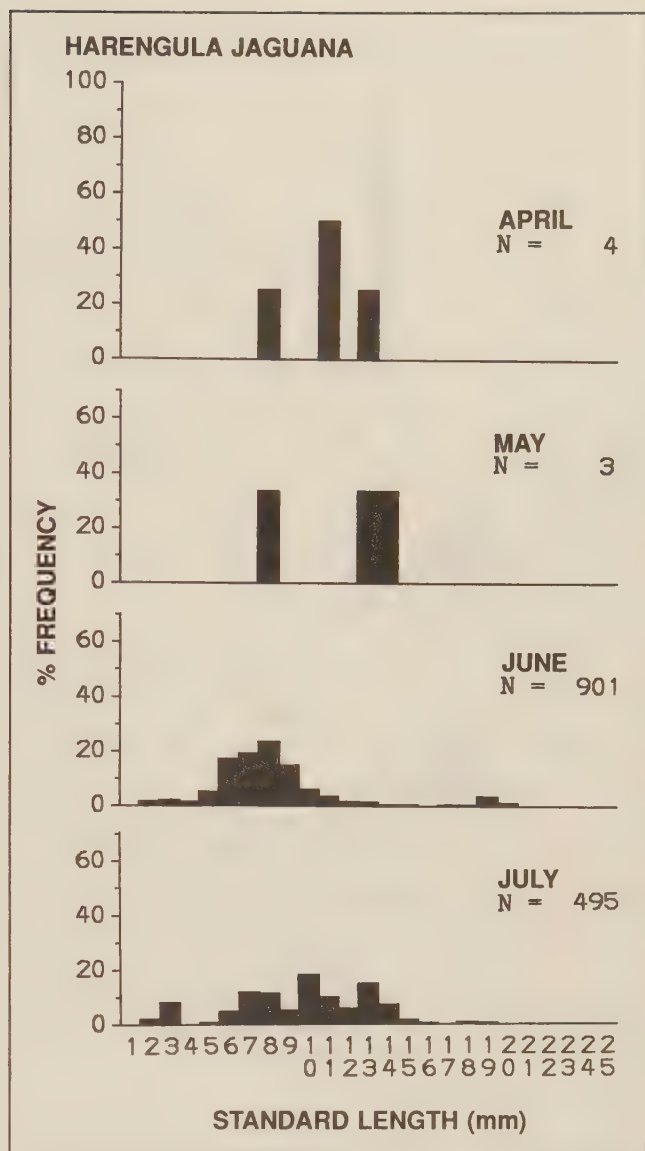


Figure 14

Monthly size-frequency distribution of *Harengula jaguana* larvae for positive-catch months during 1982 SEAMAP neuston and half-meter ring net collections. *N* = total number caught.

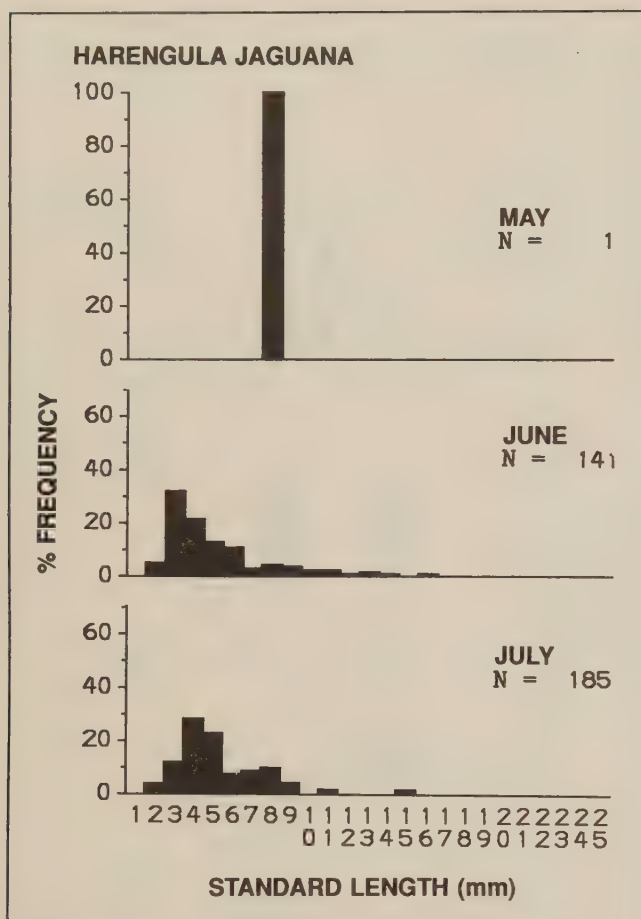


Figure 15

Monthly size-frequency distribution of *Harengula jaguana* larvae for positive-catch months during 1983 SEAMAP bongo net collections. *N* = total number caught.

Opisthonema oglinum

Larval *O. oglinum* from the Gulf of Mexico can be separated from all other clupeid genera except *Sardinella* on the basis of meristics alone (Houde and Fore 1973, Richards et al. 1974). Myomere counts between the posterior insertion of the dorsal fin and the termination of the gut (i.e., postdorsal-preanal myomeres) are the principal diagnostic character used. Those counts are much higher on *O. oglinum* (8–10 for fish <16 mm SL) than on other clupeids in the Gulf, but they overlap those of *Sardinella aurita* (5–8). For larvae less than 16 mm SL, other differences in pigmentation, morphometrics, and meristics have not been described for these two genera; consequently, we had occasional difficulties in distinguishing specimens that had 8 postdorsal-preanal myomeres. Therefore, clupeid larvae below 16 mm SL with postdorsal-preanal myomere counts clearly 9 or greater were considered to be *O. oglinum*. Larvae having counts of 8, and lacking pigmentation on the nape of the neck (frequently found on *S. aurita*, Shaw and Drullinger unpubl. data), were grouped into an *Opisthonema/Sardinella* complex and are reported separately. Larvae having 5–7 postdorsal-preanal

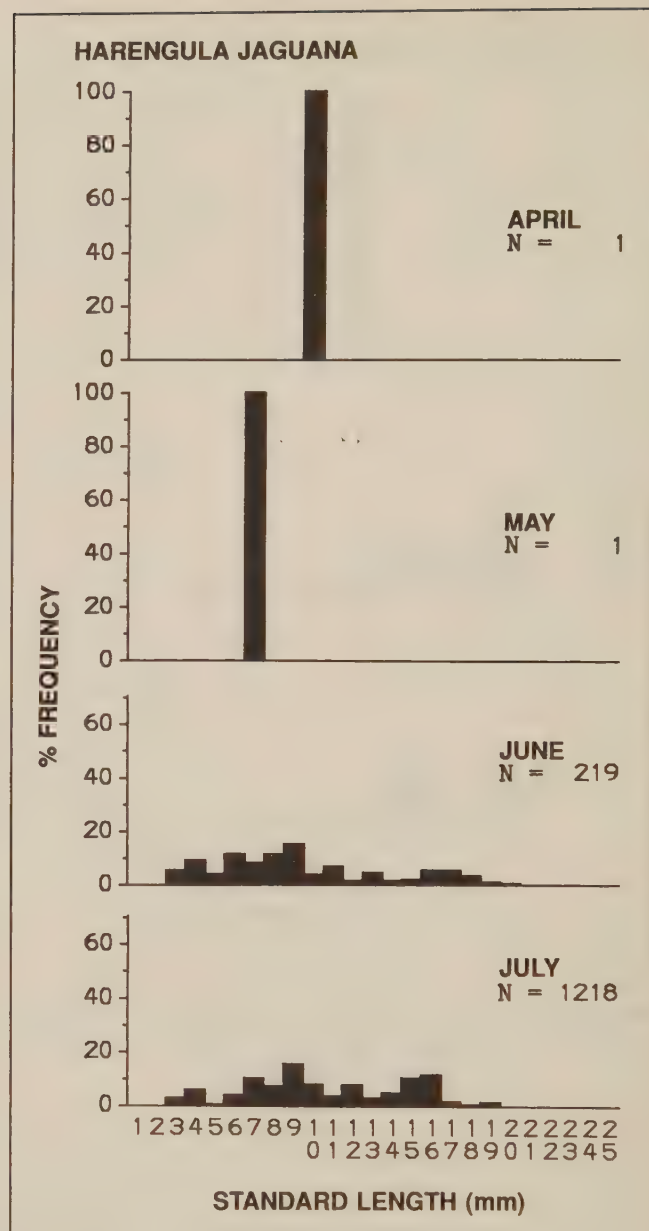


Figure 16

Monthly size-frequency distribution of *Harengula jaguana* larvae for positive-catch months during 1983 SEAMAP neuston and half-meter ring net collections. *N* = total number caught.

myomeres, or bilateral melanophores at the nape and more than 42 total myomeres, were considered to be *S. aurita*. Above 16 mm SL, fin ray counts are also diagnostic.

Opisthonema oglinum larvae were abundant in nearshore waters across the Gulf. Relatively good coverage of on-shelf stations during June in all areas except southern Texas (Figs. 17–20) revealed high larval abundances from mid-Louisiana to mid-Texas and, in 1982, over the west Florida shelf. Coverage of shelf stations was poor off southern Texas, but a few bongo tows in July revealed at least the presence of larvae. Bongo gear were consistently more effective than neuston or ring nets; during June 1982, larvae were captured

OPISTHONEMA OGILINUM

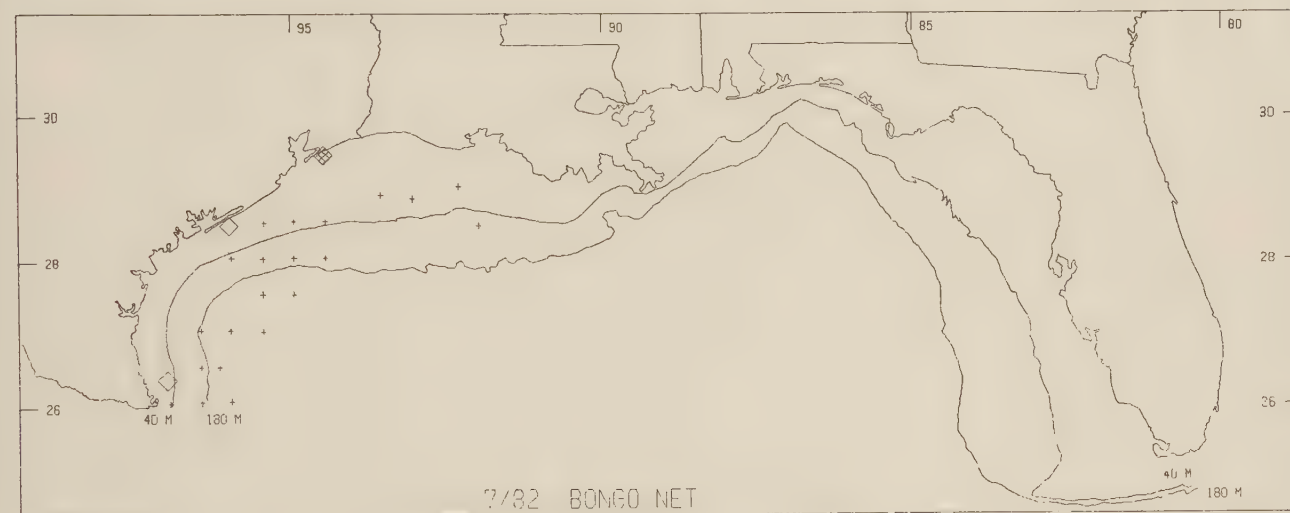


Figure 17

Distribution and abundance ($N/10 \text{ m}^2$) of *Opisthonema ogilinum* larvae for positive-catch months during 1982 SEAMAP bongo net collections. Stations sampled (+).

on the west Florida shelf in 14 of 47 bongo tows, but not in 47 neuston hauls (no ring nets were towed). Abundance was far greater on the inner shelf than on the outer shelf (Table 4). Mean depth at positive stations was 33 m in 1982 and 23 m in 1983.

Over the two years, 4862 *O. ogilinum* larvae were collected. Mean abundance was highest among the target clupeids in 1982, but dropped considerably by 1983 (Table 4). If the fish included in the *Opisthonema/Sardinella* section are in fact *O. ogilinum* (which evidence suggests, see *Opisthonema/Sardinella* section), difference in mean abundance between 1982 and 1983 is even greater than shown in Table 4. This yearly difference in mean abundance primarily reflects the difference in catch and effort during

June of the two years. For example, the two greatest single-station abundances (614 and 1488 larvae/ 10 m^2) were encountered in June 1982 south of Sabine Pass on the Texas and Louisiana border at station depths of 11 and 15 m, respectively.

OPISTHONEMA OGLINUM

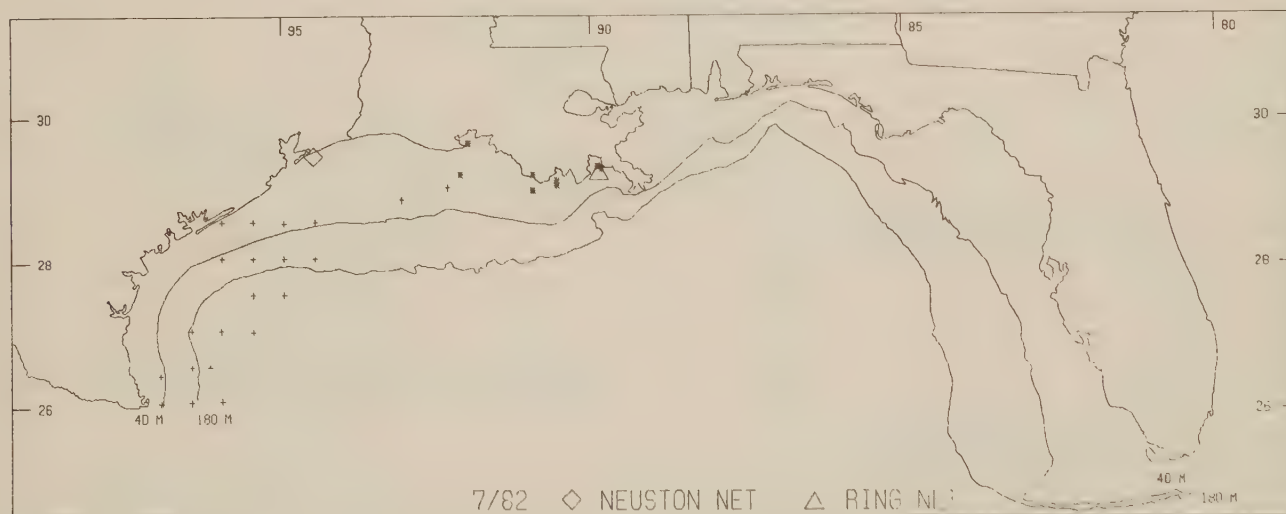


Figure 18

Distribution and CPUE (N/tow) of *Opisthonema oglinum* larvae for positive-catch months during 1982 SEAMAP neuston and half-meter ring net collections. Stations sampled: + neuston, * ring nets.

OPISTHONEMA OGLINUM

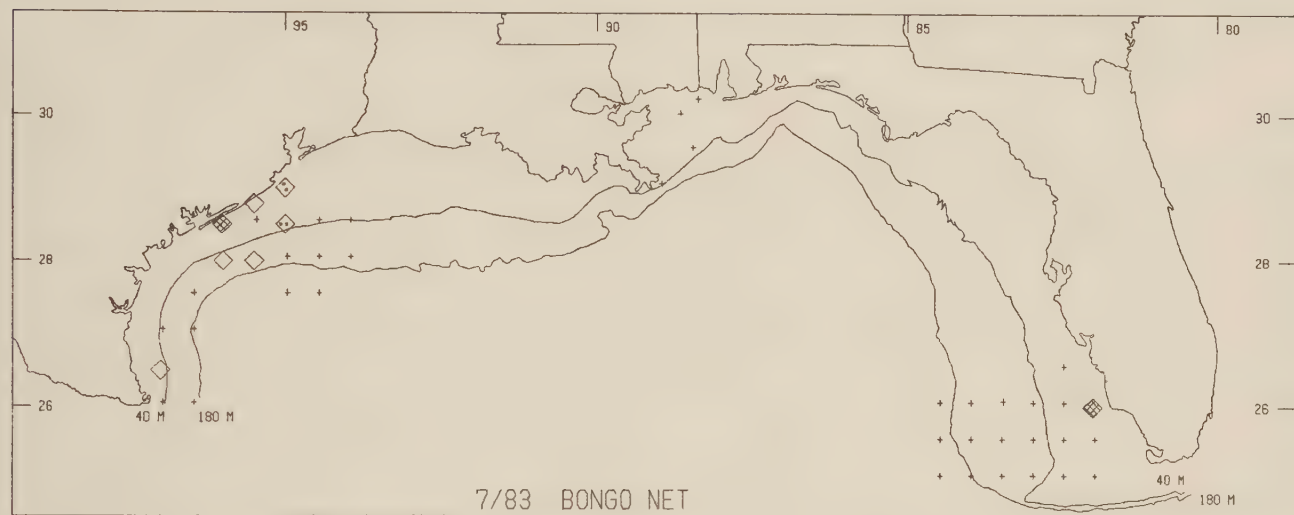


Figure 19

Distribution and abundance ($N/10 \text{ m}^2$) of *Opisthonema oglinum* larvae for positive-catch months during 1983 SEAMAP bongo net collections. Stations sampled (+).

OPISTHONEMA OGLINUM

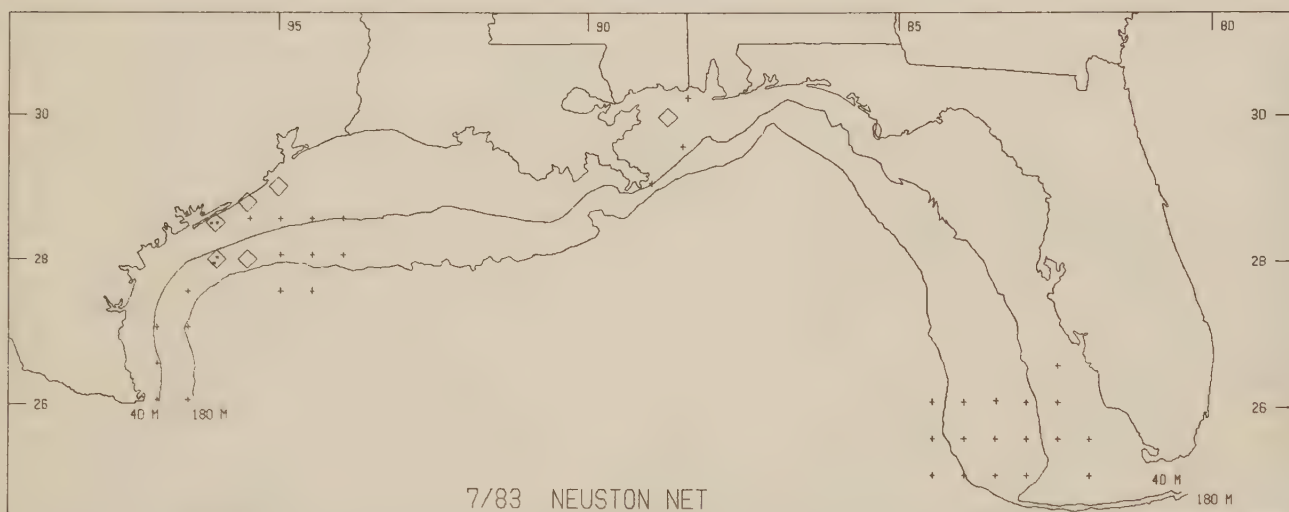


Figure 20

Distribution and CPUE (N/tow) of *Opisthonema oglinum* larvae for months with positive neuston catches during 1983 SEAMAP neuston and half-meter ring net collections. Stations sampled: + neuston, * ring nets. No larvae taken in ring nets.

All larvae were collected in June and July (Table 8). Length-frequency data indicate no clear modal progression toward larger larvae from June to July (Figs. 21–24).

Surface temperatures and salinities at stations where recently hatched larvae (<4.0 mm SL) were captured were 27.0°–30.5°C and 21.2–36.6 ppt (Table 6). Surface temperature and salinity ranges for all sizes of larvae collected were 20.6°–32.0°C and 12.1–36.6 ppt. Mean values for surface waters at positive stations for all sizes of larvae were 28.9°C and 31.8 ppt in 1982, and 27.8°C, but only 25.1 ppt, in 1983.

Table 8

Opisthonema oglinum mean larval abundance ($N/10\text{ m}^2$) as determined from metered bongo tows, and mean catch-per-unit-effort (number captured/tow) as determined from neuston and unmetered 0.5-m ring net tows for positive-catch stations only. Spawning season considered to be February–November (Ditty et al. 1988; this work). For total SEAMAP yearly sampling effort by month, gear type, and depth, see Table 3.

Mean variable	June	July
Bongo catch		
1982	108.5 ¹ (23/102)	30.0 (3/26)
1983	9.8 (7/55)	17.8 (8/44)
Neuston or ring catch		
1982	135.4 (7/120)	4.0 (2/45)
1983	4.7 (3/88)	15.7 (6/42)
Surface salinity (ppt)		
1982	31.8 ² (21–37)	32.8 (26–36)
1983	20.5 (12–32)	25.7 (23–35)
Surface temperature (°C)		
1982	28.8 (27–30)	29.4 (28–32)
1983	26.9 (25–29)	28.2 (21–30)
Station depth (m) ³		
1982	36 (6–540)	16 (9–33)
1983	16 (9–24)	27 (9–53)

¹Frequency of occurrence: number of positive-catch stations over number of stations samples.

²Range of values.

³Sampling methodology for bongo nets limits tows to upper 200 m of water (see Methods section).

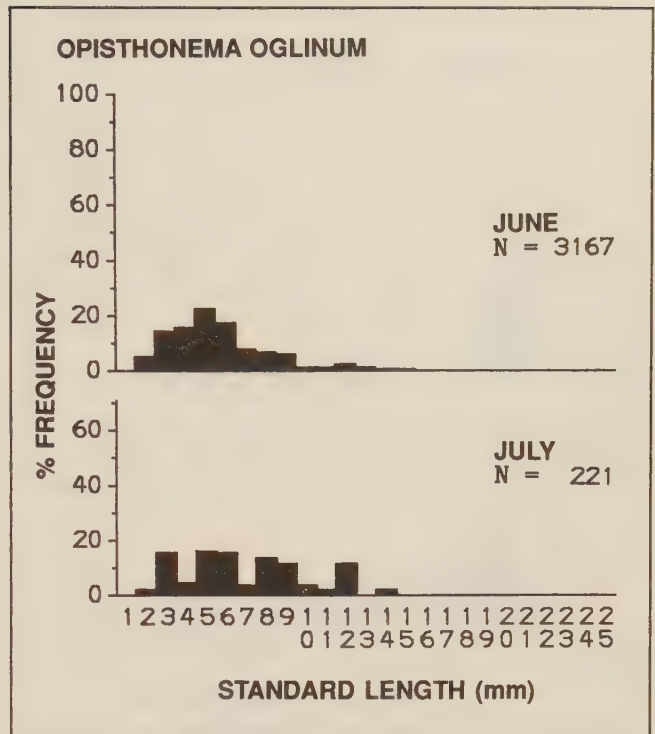


Figure 21

Monthly size-frequency distribution of *Opisthonema oglinum* larvae for positive-catch months during 1982 SEAMAP bongo net collections. N = total number caught.

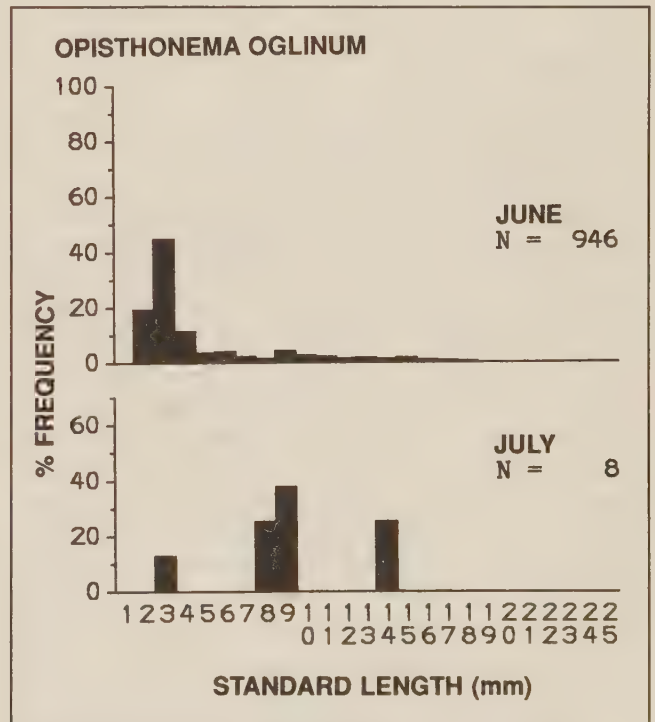


Figure 22

Monthly size-frequency distribution of *Opisthonema oglinum* larvae for positive-catch months during 1982 SEAMAP neuston and half-meter ring net collections. N = total number caught.

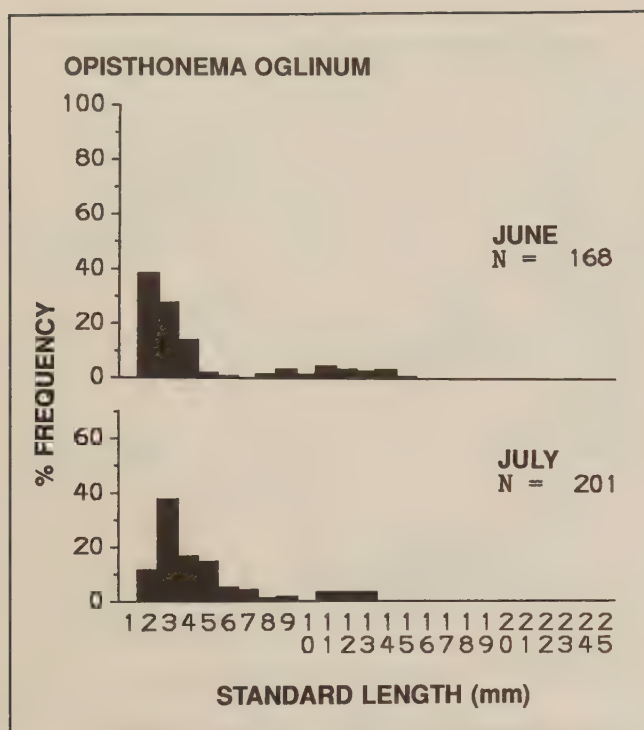


Figure 23

Monthly size-frequency distribution of *Opisthonema oglinum* larvae for positive-catch months during 1983 SEAMAP bongo net collections.
N = total number caught.

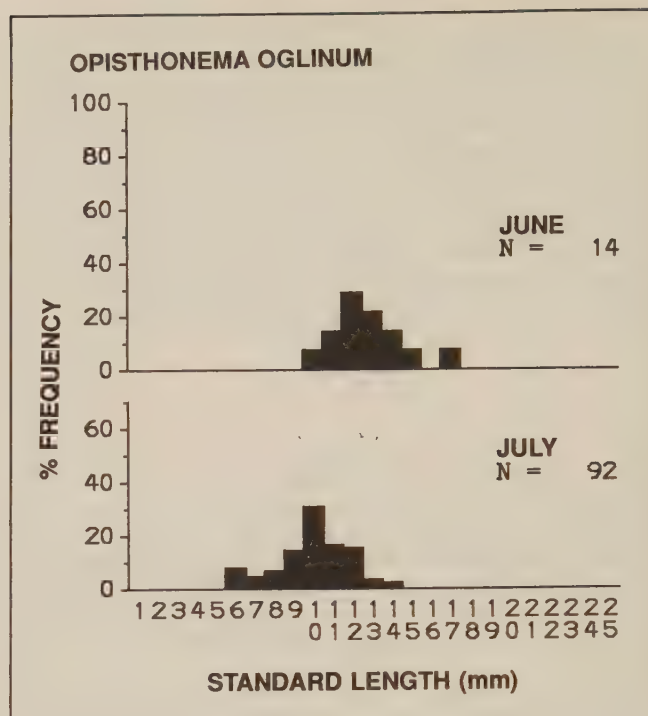


Figure 24

Monthly size-frequency distribution of *Opisthonema oglinum* larvae for positive-catch months during 1983 SEAMAP neuston net collections.
N = total number caught.

Sardinella aurita

Spanish sardine larvae were abundant in the shelf waters off west Florida. Highest abundances were generally along and inshore of the 40-m contour. These larvae also occurred to a much lesser extent off eastern Texas and western Louisiana (Figs. 25–28). Coverage of shelf stations was poor off the southern half of Texas, but indicated that larvae occur off its southern tip during July. Positive-catch stations for *S. aurita* larvae within the 183-m contour during 1982 and 1983 had mean depths of 32.6 and 34.3 m, respectively.

During 1982 and 1983, 16,470 *S. aurita* larvae were collected. Of those, 13,302 were collected in 1982 alone; however, 9828 came from two neuston net hauls north of Tampa Bay, Florida, during mid-June. Though greater numbers of larvae were collected in 1982 than in 1983, mean gulfwide abundances from bongo collections were greater in 1983. *Sardinella aurita* larvae were the only target clupeid to show increased abundances in 1983. This occurred on the inner shelf only, where larvae were most abundant (Table 4). Further offshore, abundance decreased from 1982 to 1983. Gulfwide, *S. aurita* was the most abundant of the target clupeids in 1983. In Florida waters only, they were by far the most abundant larval clupeid during both 1982 and 1983; mean abundances in inner-shelf waters east of Apalachicola were 79.8 and 352.5 fish/10 m², respectively.

Sardinella aurita larvae were collected 17 April–23 November (Table 9). In April and May, station coverage on the shelf was limited, and larvae were sparse in offshore samples. Occasional patches of larvae 6–15 mm SL were found off the west Florida shelf and out to the central Gulf. Spawning occurred on the west Florida shelf during May and possibly April, as indicated by concentrations of larvae 5.5–18.7 mm SL off Crystal River in May 1983. Recently hatched larvae (<4.0 mm) were taken in June and July only, between the 10- and 65-m depth contours (mean depth 27 m) along Florida's entire Gulf coast and off eastern and southern Texas. Larvae less than 8 mm SL were captured each month larvae were taken except November (Figs. 29–32), indicating a protracted spawning season. A few larvae were taken in October and November from the northern Gulf, which was the only area sampled then.

Surface temperatures and salinities at locations where recently hatched larvae (<4.0 mm SL) were captured were 27.2°–29.7°C and 24.8–36.5 ppt (Table 6). Surface temperature and salinity ranges for all sizes of larvae were 21.2°–30.8°C and 24.1–36.8 ppt. Mean values for surface waters at all positive stations were 28.3°C and 34.9 ppt in 1982, and 26.7°C and again 34.9 ppt in 1983. Neuston net hauls accounted for 85% of the *S. aurita* larvae captured in 1982, but only 36% in 1983; the remainder were captured in bongos.

SARDINELLA AURITA

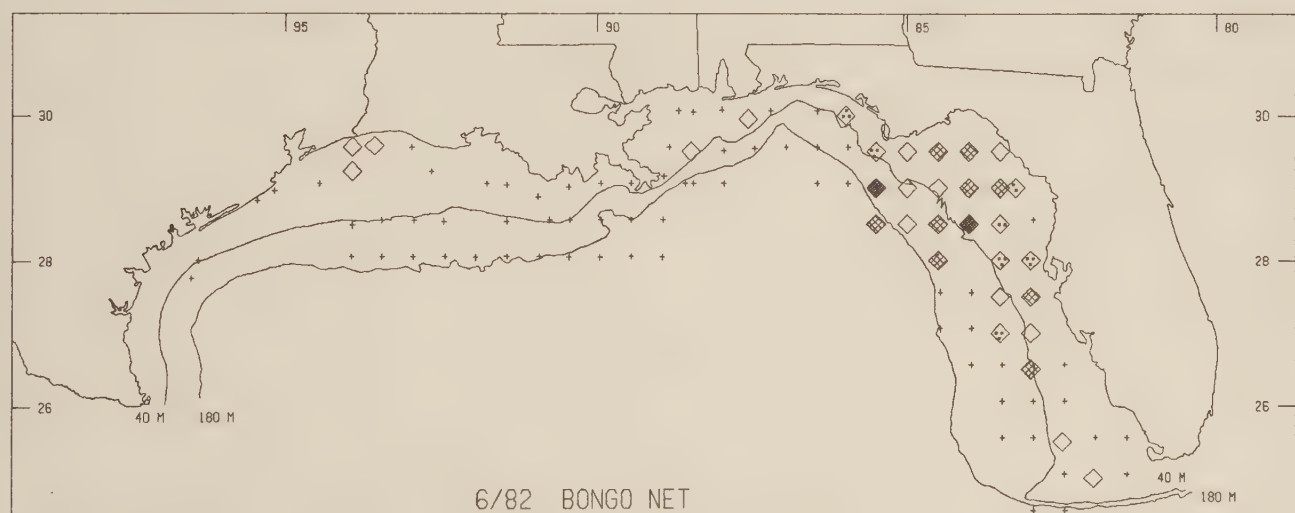
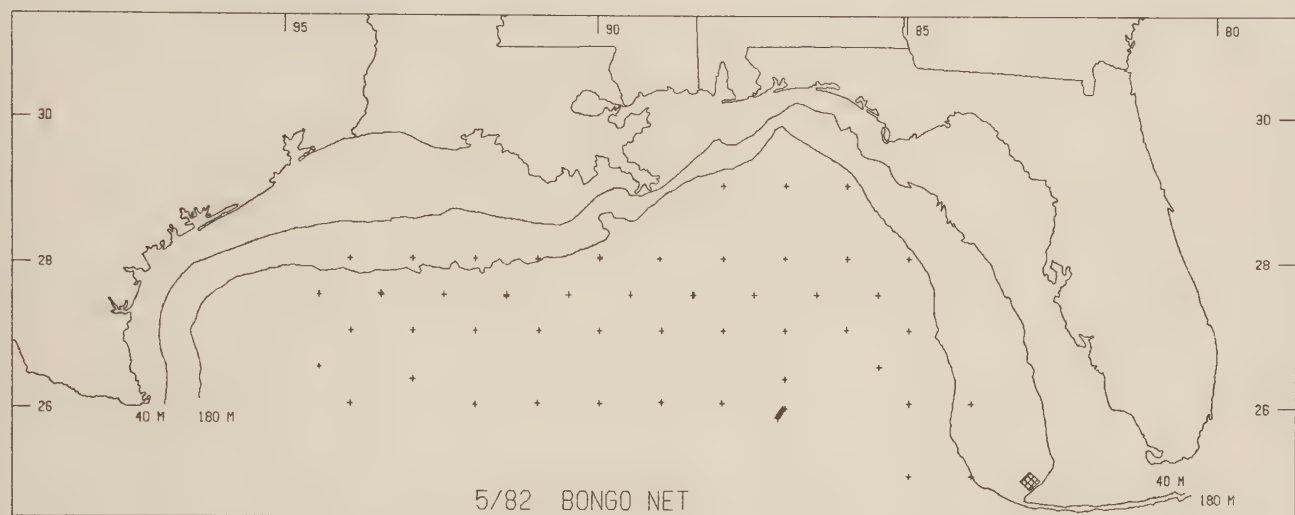
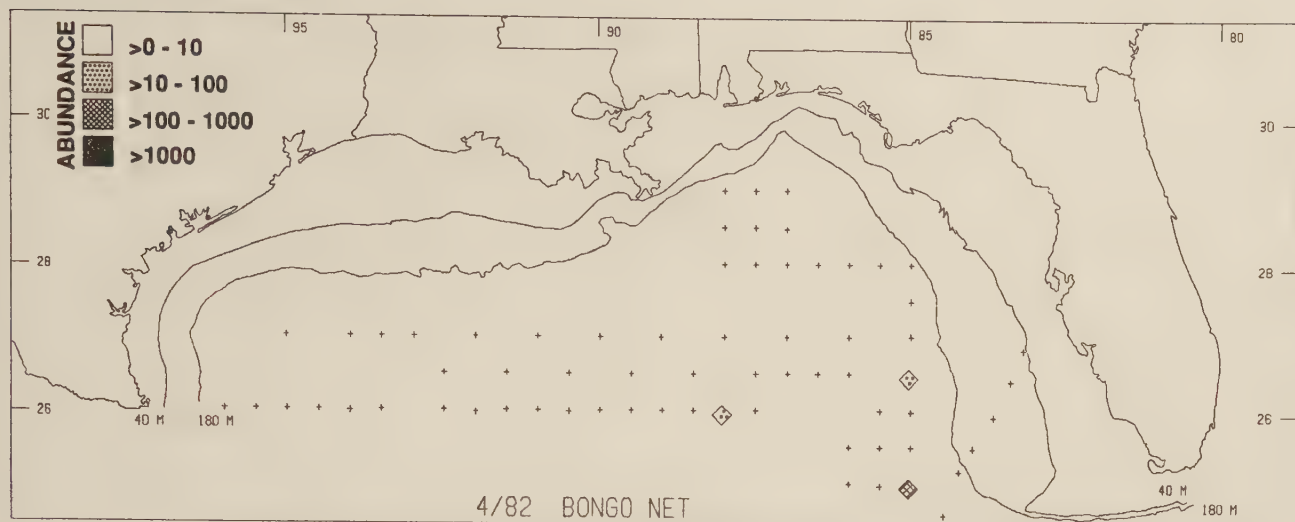


Figure 25

Distribution and abundance ($N/10 \text{ m}^2$) of *Sardinella aurita* larvae for positive-catch months during 1982 SEAMAP bongo net collections. Stations sampled (+).

SARDINELLA AURITA

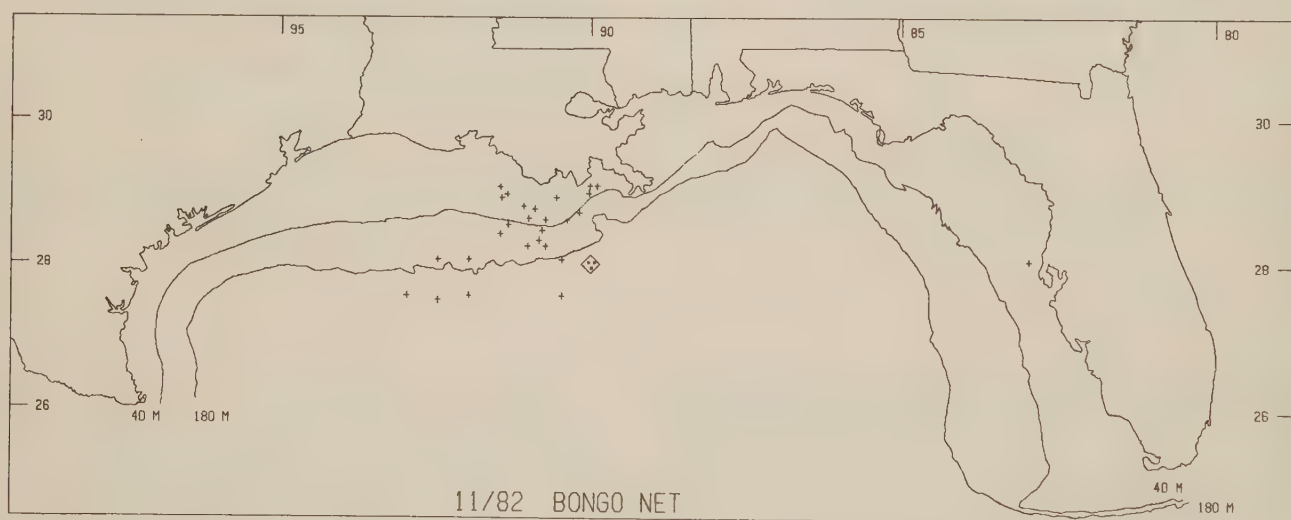
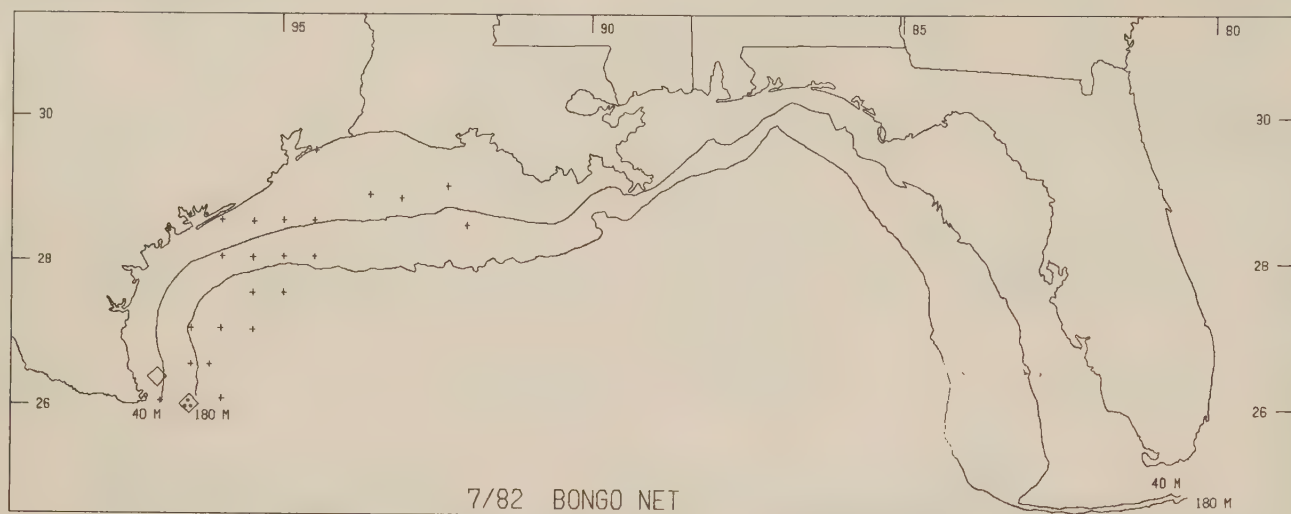


Figure 25 (continued)

SARDINELLA AURITA

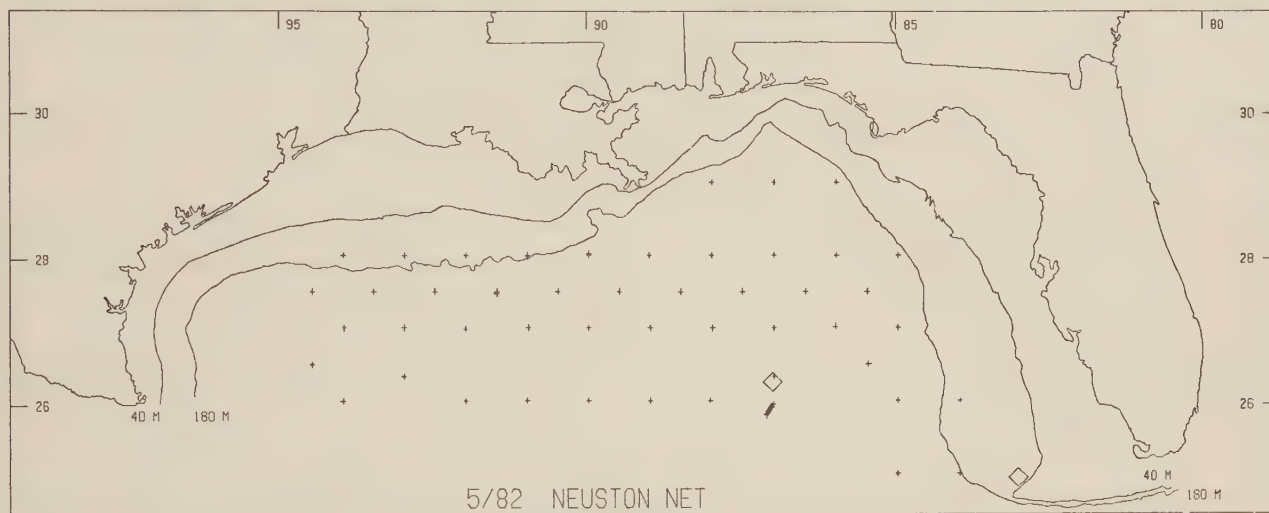
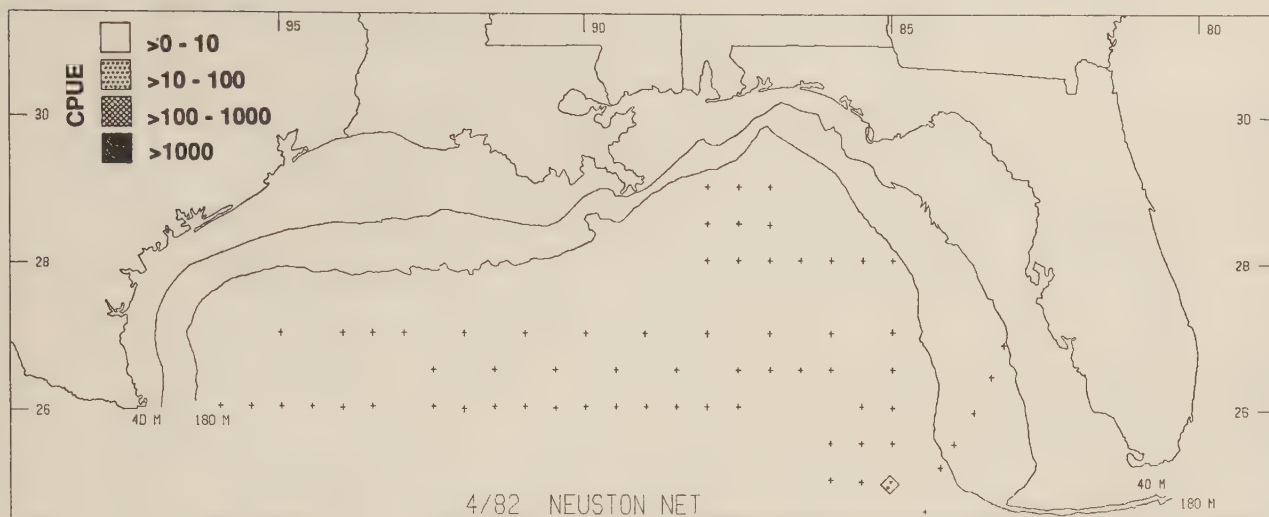


Figure 26

Distribution and CPUE (N/tow) of *Sardinella aurita* larvae for months with positive neuston catches during 1982 SEAMAP neuston and half-meter ring net collections. Stations sampled: + neuston, * ring nets. No larvae taken in ring nets.

SARDINELLA AURITA

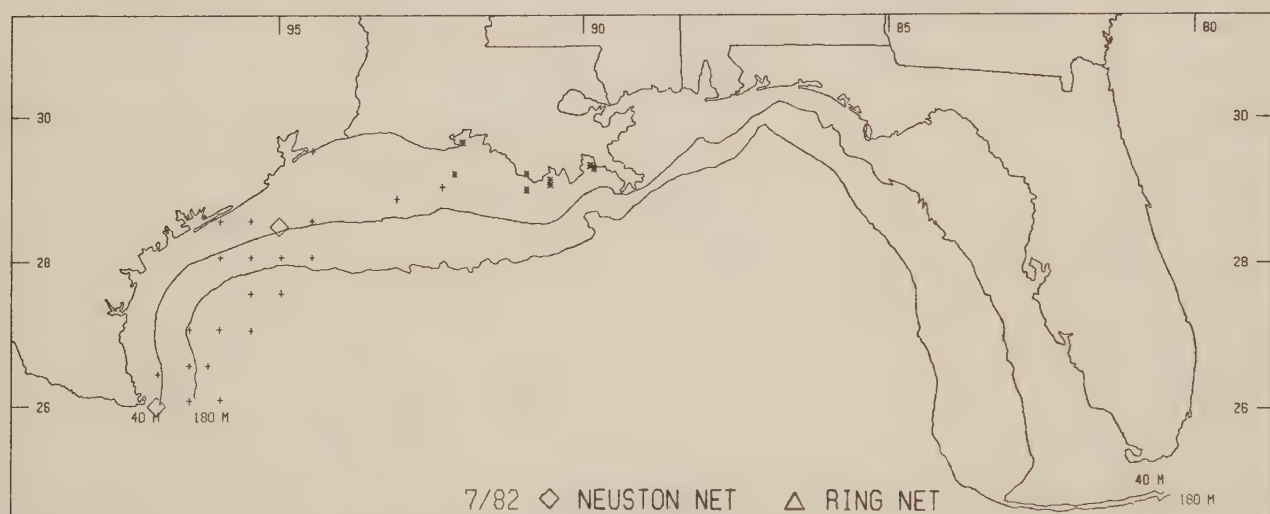
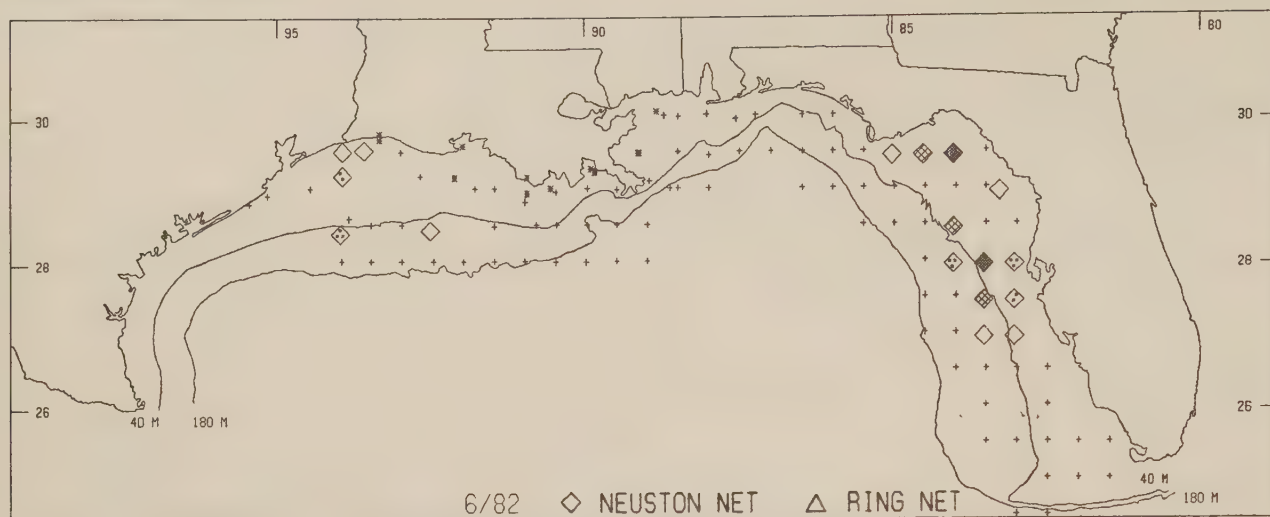


Figure 26 (continued)

SARDINELLA AURITA

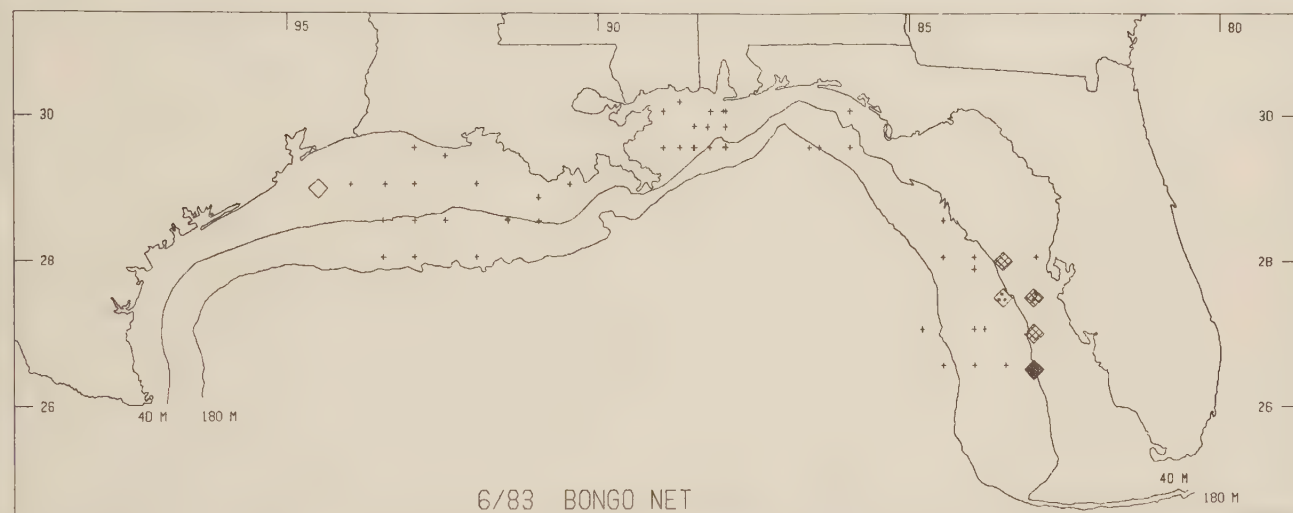
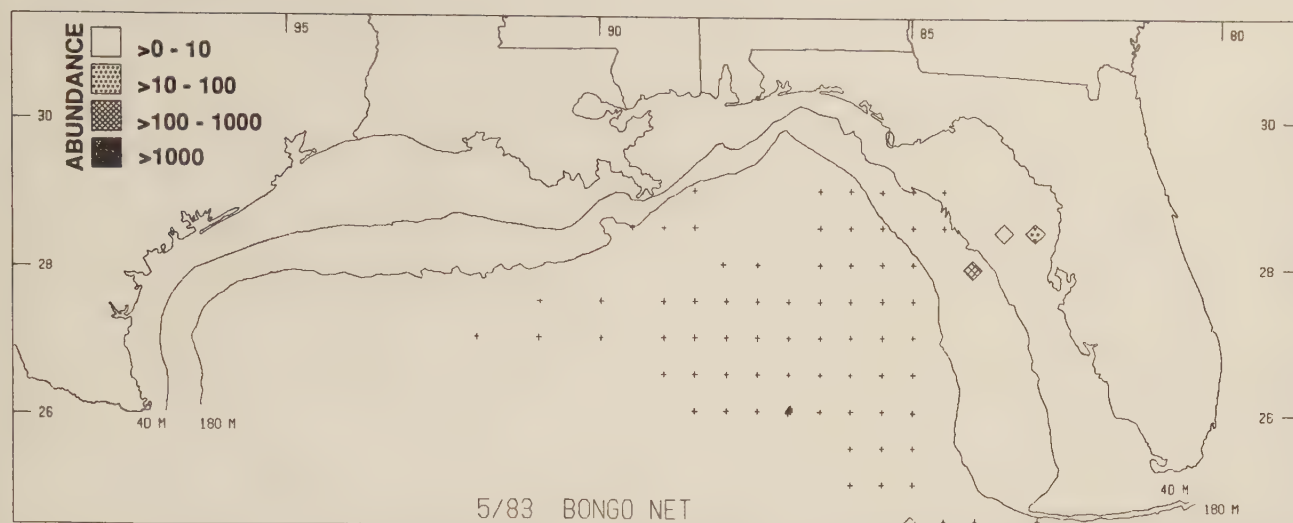


Figure 27

Distribution and abundance ($N/10\text{ m}^2$) of *Sardinella aurita* larvae for positive-catch months during 1983 SEAMAP bongo net collections. Stations sampled (+).

SARDINELLA AURITA

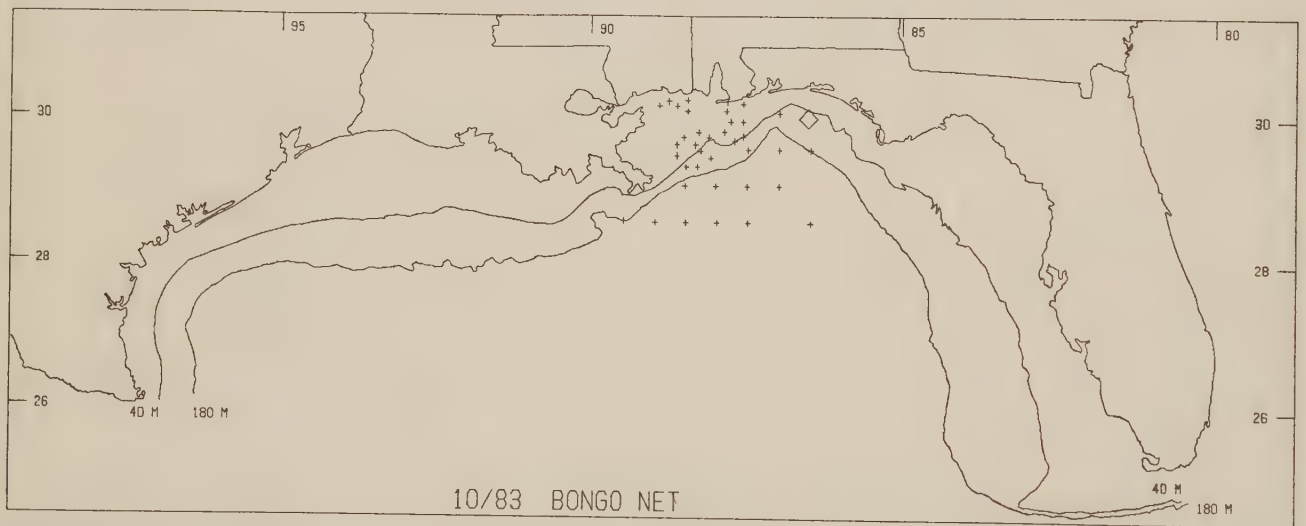
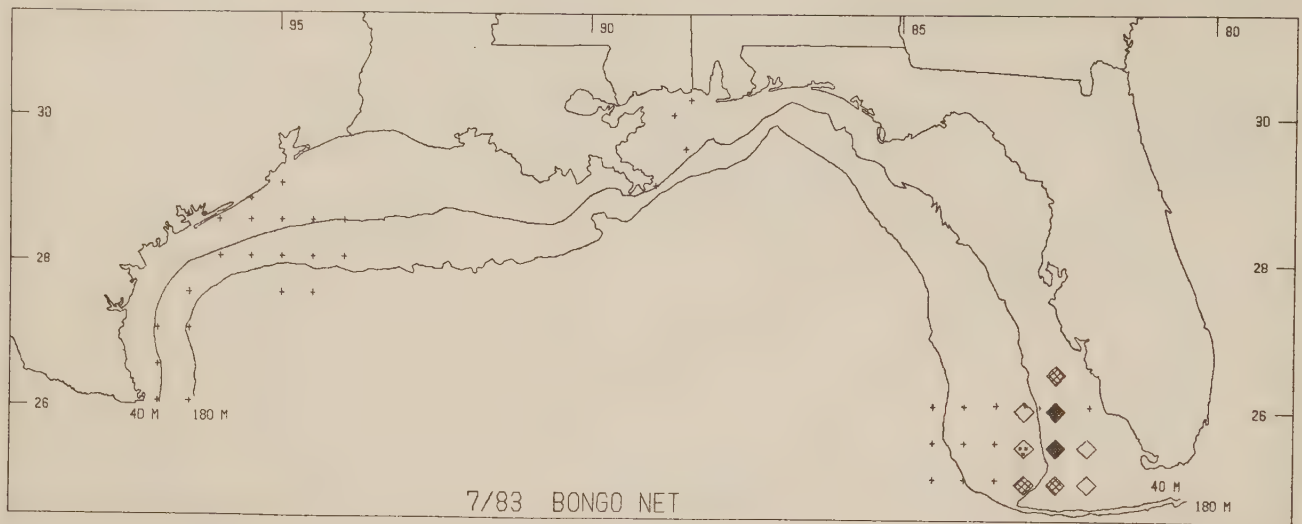


Figure 27 (continued)

SARDINELLA AURITA

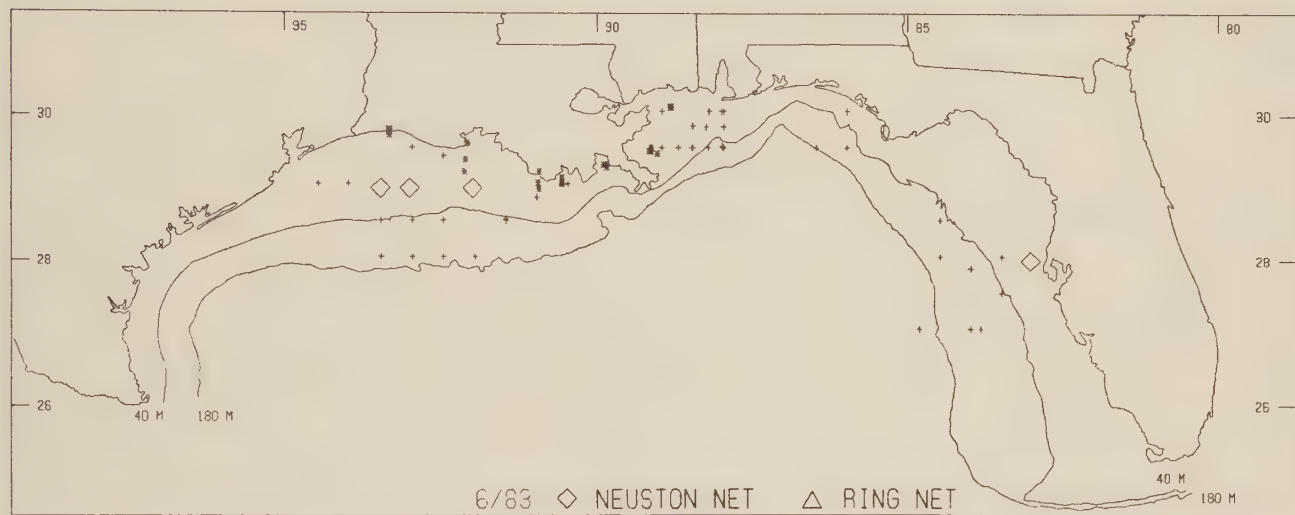
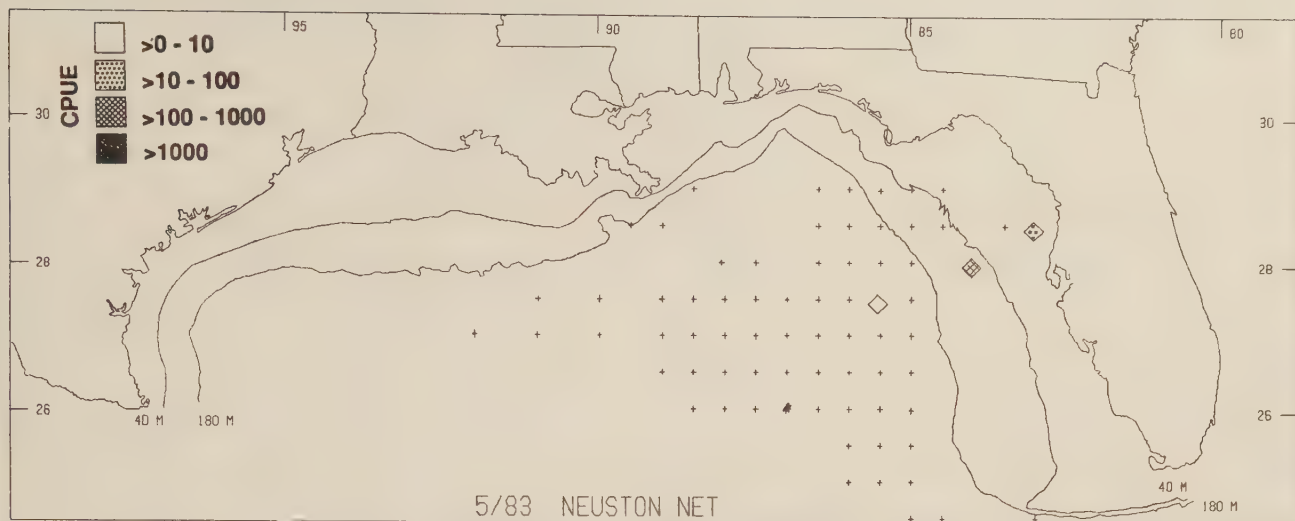


Figure 28

Distribution and CPUE (N/tow) of *Sardinella aurita* larvae for months with positive neuston catches during 1983 SEAMAP neuston and half-meter ring net collections. Stations sampled: + neuston, * ring nets. No larvae taken in ring nets.

SARDINELLA AURITA

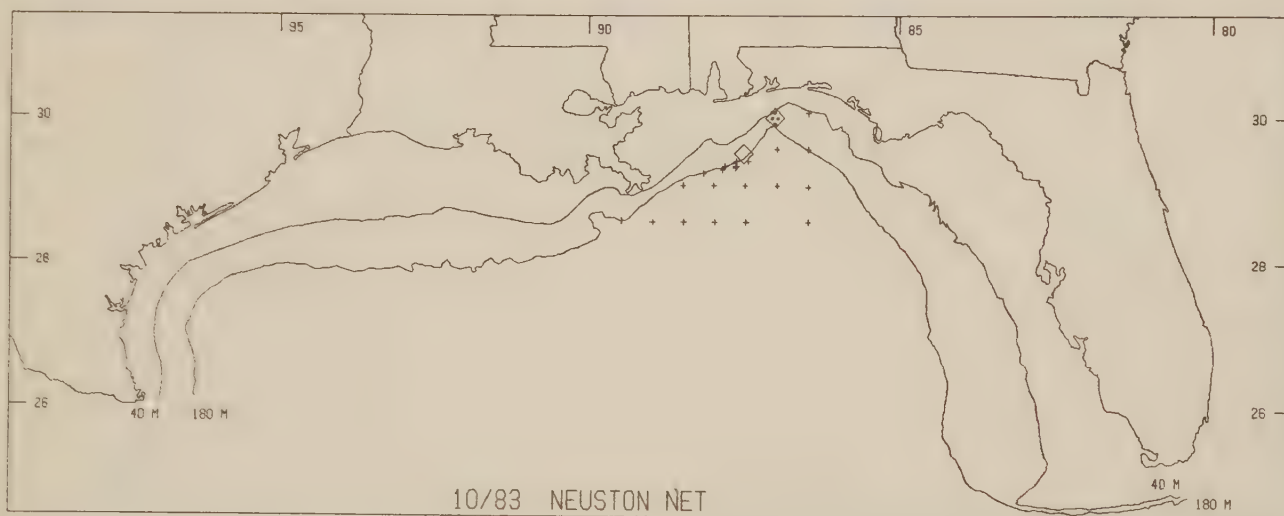
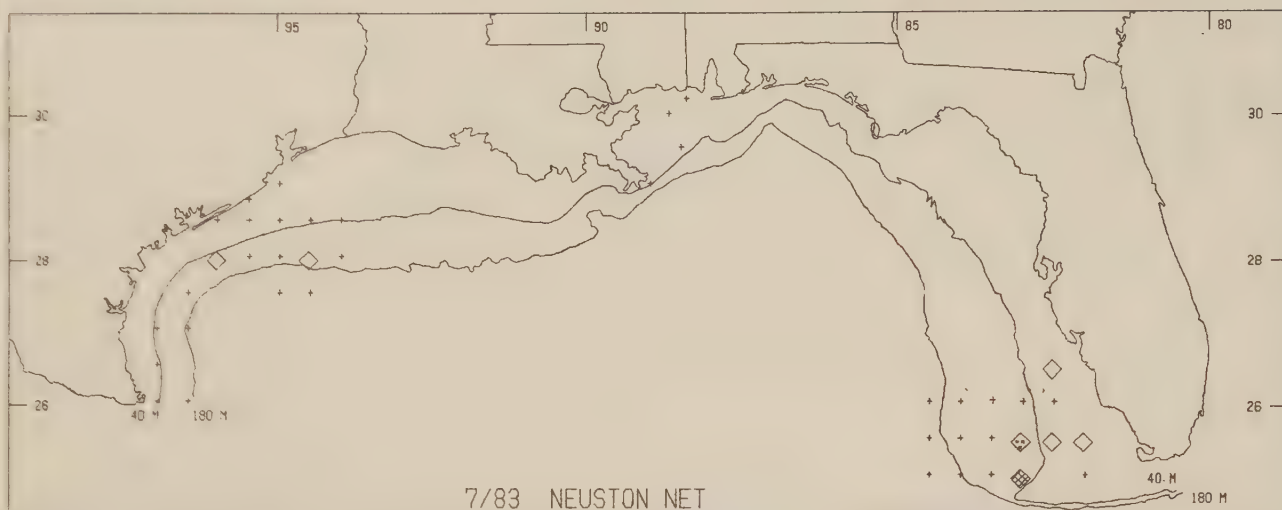


Figure 28 (continued)

Table 9

Sardinella aurita mean larval abundance ($N/10\text{ m}^2$) as determined from metered bongo tows, and mean catch-per-unit-effort (number captured/tow) as determined from neuston and unmetered 0.5-m ring net tows for positive-catch stations only. Spawning season considered to be year-round (Ditty et al. 1988; this work). For total SEAMAP yearly sampling effort by month, gear type, and depth, see Table 3.

NS = no samples taken.

Mean variable	April	May	June	July
Bongo catch				
1982	5.1 ¹ (3/69)	4.7 (1/71)	63.6 (32/102)	0.9 (2/26)
1983	0.0 (0/27)	14.0 (4/84)	58.0 (6/55)	66.7 (9/44)
Neuston or ring catch				
1982	26.0 (1/68)	2.0 (2/73)	625.5 (18/120)	2.5 (2/45)
1983	0.0 (0/27)	142.3 (3/82)	1.5 (4/88)	98.7 (7/42)
Surface salinity (ppt)				
1982	36.4 ² (36–37)	36.4 (36–37)	34.8 (28–37)	35.4 (33–36)
1983		36.0 (34–37)	32.9 (25–36)	35.3 (24–37)
Surface temperature (°C)				
1982	27.3 (27–28)	26.0 (26–27)	28.5 (27–30)	28.8 (27–31)
1983		22.4 (21–26)	27.9 (27–30)	28.0 (24–30)
Station depth (m) ³				
1982	2793 (1620–3294)	1072 (52–3111)	33 (6–188)	40 (27–65)
1983		742 (22–3396)	26 (13–40)	36 (18–68)
	August	September	October	November
Bongo catch				
1982	NS	NS	0.0 (0/3)	1.3 (1/29)
1983	NS	NS	0.2 (1/39)	NS
Neuston or ring catch				
1982	NS	NS	0.0 (0/8)	0.0 (0/3)
1983	NS	NS	9.5 (2/25)	NS
Surface salinity (ppt)				
1982				36.5
1983			35.4 (35–36)	
Surface temperature (°C)				
1982				
1983			25.6 (25–26)	
Station depth (m) ³				
1982				540
1983			63 (54–71)	

¹Frequency of occurrence: number of positive-catch stations over number of stations sampled.

²Range of values.

³Sampling methodology for bongo nets limits tows to upper 200 m of water (see Methods section).

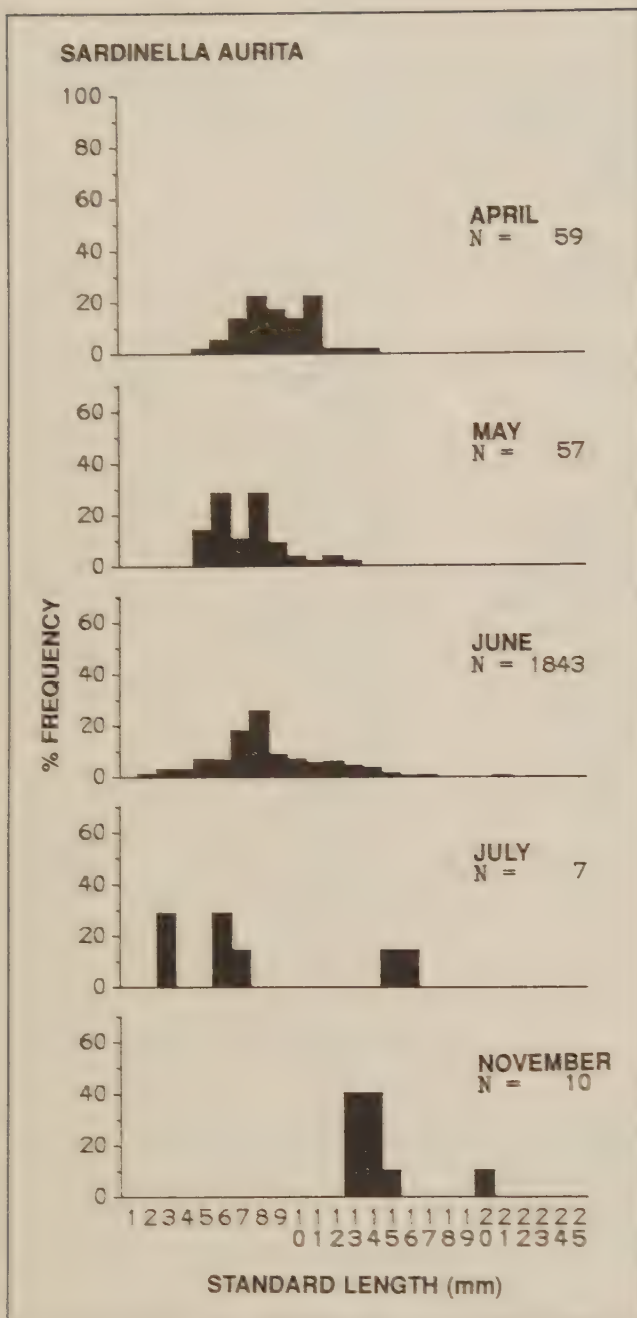


Figure 29

Monthly size-frequency distribution of *Sardinella aurita* larvae for positive-catch months during 1982 SEAMAP bongo net collections.
N = total number caught.

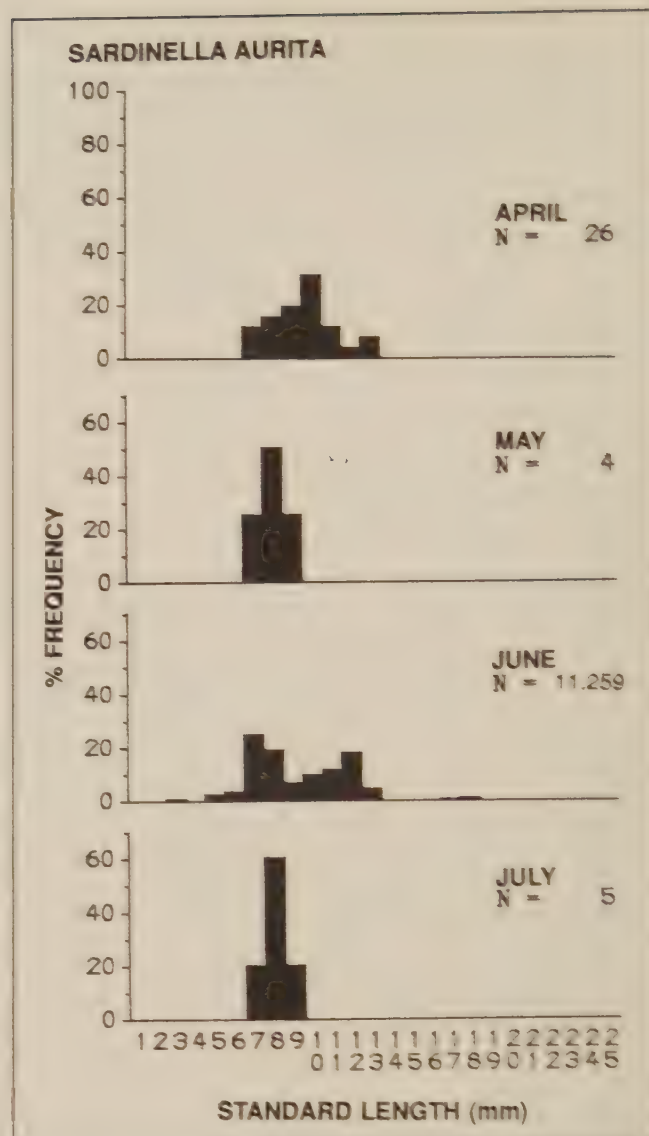


Figure 30

Monthly size-frequency distribution of *Sardinella aurita* larvae for positive-catch months during 1982 SEAMAP neuston net collections.
N = total number caught.

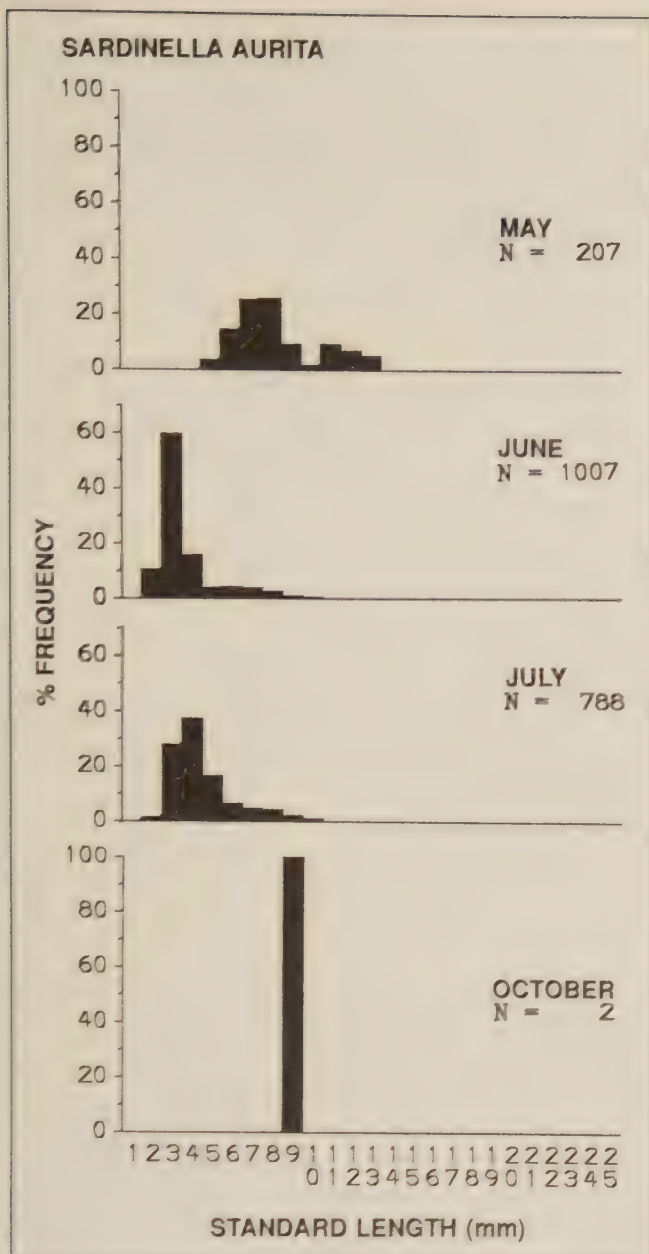


Figure 31

Monthly size-frequency distribution of *Sardinella aurita* larvae for positive-catch months during 1983 SEAMAP bongo net collections.
N = total number caught.

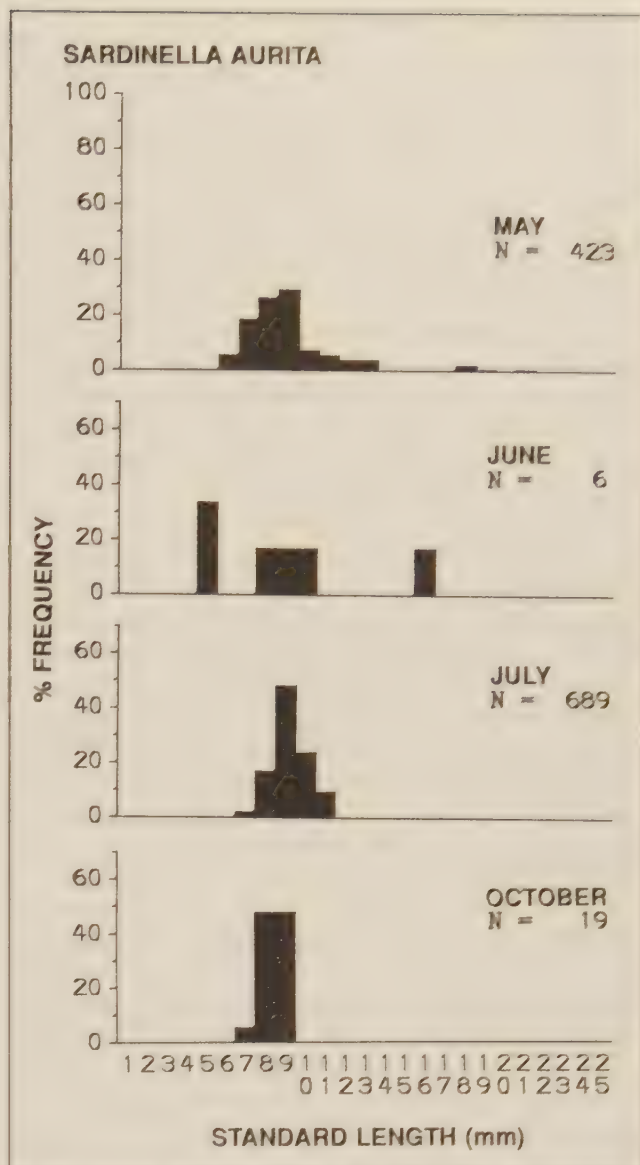


Figure 32

Monthly size-frequency distribution of *Sardinella aurita* larvae for positive-catch months during 1983 SEAMAP neuston net collections.
N = total number caught.

Opisthonema/Sardinella

Original analysis of the 1982 data yielded 6044 larvae that could be identified only to the generic group *Opisthonema/Sardinella*. Upon reexamination of that group, 43% were classified as *O. oglinum* (those are included with the data on *O. oglinum*). Less than 1% of those reexamined were classified as *S. aurita*. Probably the remainder of the generic group is predominantly *O. oglinum* as well. However, identifications were hampered by overlapping meristic values, similar pigmentation characteristics, and, in some instances, poor larval condition. During the 1983 analysis, a greater percentage of *Opisthonema* and *Sardinella* larvae were successfully identified to the species level, but a total of 5091 larvae remain grouped into the *Opisthonema/Sardinella* complex from 1982 and 1983 collections.

Larvae of the generic group were captured only during June and July of both years (Table 10), months when both *S. aurita* and *O. oglinum* were most abundant. Larvae were collected off central Louisiana, where *S. aurita* were rare, however, they were also taken off east Texas and southern Florida, where *S. aurita* and *O. oglinum* were likely to be found together. Salinities, temperatures, and water depths at sites where recently hatched larvae were captured resembled the values at capture sites for small *O. oglinum* during 1983, but were much more similar to those at capture sites for small *S. aurita* during 1982 (Table 6).

Discussion

The common coastal pelagic clupeids of the northern Gulf of Mexico can be divided into two groups: warm-water (summer) and cold-water (winter) spawners (Houde and Fore 1973). The "summer" spawners are *Harengula jaguana*, *Opisthonema oglinum*, and *Sardinella aurita*. Their larvae are common during May–August and in this study were often captured together, especially those of *H. jaguana* and *O. oglinum*. The "winter" spawned larvae of *Etrumeus teres* and *Brevoortia patronus* are also common and often caught together, especially during January–March in waters of the north-central Gulf (Ditty 1986, Ditty et al. 1988).

Etrumeus teres adults differ from the "summer-spawning" pelagic clupeids in that they appear to concentrate much of their spawning beyond the 40-m depth contour (Tables 4 and 6) at least during late February through May. Adult *E. teres* are generally distributed along the outer continental shelf and slope (Bullis et al. 1971, Klima 1971, Reintjes 1979a), and larval distributions indicate that they spawn in that area as well. Larvae were also found off the continental shelf. Previous larval studies generally did not extend beyond the outer shelf (Fore 1971, Houde 1977a, Finucane et al. 1979, Ditty and Truesdale 1984), so little was known about the offshore distribution of *E. teres* larvae. We found larvae less than 4.0 mm SL (alcohol preserved) in water temperatures as low as 16.7°C, as compared with a previously reported low of 20.5°C for fish less than 5.0 mm SL (Houde 1977a).

Table 10

Opisthonema/Sardinella mean larval abundance ($N/10 \text{ m}^2$) as determined from metered bongo tows, and mean catch-per-unit-effort (number captured/tow) as determined from neuston and unmetered 0.5-m ring net tows for positive-catch stations only. Spawning season considered to be February–November for *O. oglinum* and year-round for *S. aurita* (Ditty et al. 1988). For total SEAMAP yearly sampling effort by month, gear type, and depth, see Table 3.

Mean variable	June	July
Bongo catch		
1982	116.5 ¹ (16/102)	1.6 (1/26)
1983	5.7 (4/55)	5.2 (4/44)
Neuston or ring catch		
1982	262.8 (5/120)	123.0 (1/45)
1983	8.8 (5/88)	3.3 (3/42)
Surface salinity (ppt)		
1982	33.5 ² (17–37)	34.2 (33–35)
1983	22.7 (15–32)	32.3 (25–36)
Surface temperature (°C)		
1982	28.7 (28–31)	30.0 (28–32)
1983	27.1 (25–29)	29.0 (28–30)
Station depth (m) ³		
1982	25 (7–109)	14 (11–16)
1983	13 (2–37)	21 (12–32)

¹Frequency of occurrence: number of positive-catch stations over number of stations sampled.

²Range of values.

³Sampling methodology for bongo nets limits tows to upper 200 m of water (see Methods section).

Overall relative abundance of larval *E. teres* was similar to those of the other clupeids. Abundance on the inner shelf may be misleadingly low, however, because mean abundance calculations were based on catches at inshore stations, of which many were sampled after the peak spawning period for adult *E. teres*. Inshore abundances for the "summer-spawned" larval clupeids were probably more representative of actual values because most inshore stations were sampled during the summer months and, therefore, provide better coverage of the peak spawning areas and seasons for those species. Relative to the three other clupeids, *E. teres* ranked lowest in inshore abundance, but may actually be much more abundant than is evident here.

Larvae of the "summer" clupeids are spawned primarily on the inner shelf (Houde 1973). On the west Florida shelf, *S. aurita* larvae are clearly the most abundant clupeid and reportedly the most abundant of all species of west Florida pelagic fish larvae (Houde et al. 1979). Though *S. aurita* larval abundance has been shown to vary annually by a factor of 20 (Houde et al. 1979), our differences in abundance for 1982 and 1983 were considerably lower. Variability by month between years appeared high (Table 9), but much of this was caused by yearly variability in sampling effort and location. For example, during July 1983, sample coverage was thorough off southwest Florida and accounted for a high abundance of larvae that month, but that same area was not sampled in July 1982.

Although this study confirmed that *S. aurita* spawning is protracted, and that most spawning occurs on the inner shelf during spring and summer, spawning covers a greater geographic area than previously documented. Some adults may migrate offshore during winter (Grall 1984), and the presence of larvae (5–14 mm SL) far off the shelf during April implies that spawning may occur within that offshore population. Winter spawning, which was known to occur off southwest Florida (Houde et al. 1976, 1979), may also occur to a limited extent in the northern Gulf when water temperatures remain above 20°–21°C, the lowest temperatures at which larvae have been collected (see Appendix). Larvae were collected during October and November in our northern Gulf samples, but water temperatures were not available for the November cruise.

Sardinella aurita larvae were occasionally found with *H. jaguana* and *O. oglinum* larvae in summertime samples off Florida, but the latter two species are more commonly found in the north-central Gulf. In Florida waters, *S. aurita* generally spawns at salinities greater than 35 ppt (Houde et al. 1976, 1979; Collins and Finucane 1984). This study included areas where inner-shelf salinities were greatly affected by freshwater inputs from the Mississippi and Sabine rivers. In those areas, recently hatched larvae were often taken at surface salinities of 25–35 ppt. Still, *S. aurita* larvae were often associated with much higher salinities than either *H. jaguana* or *O. oglinum* (Table 6).

Harengula jaguana and *O. oglinum* have very similar distributions; both are abundant off Louisiana, Mississippi, and Alabama. Overall abundance is greater for *O. oglinum* than for *H. jaguana*, but the latter were found at a higher percentage of stations (bongo and surface tows) than any of the other clupeids that were studied. *Harengula jaguana* is rarely found in dense concentrations, but has the most widespread and uniform distribution of the target species. These findings are similar to those for adult *H. jaguana*, which are also widespread inshore and generally found in small schools (Low 1973). This dispersed distribution and small school size differs from the often clumped and large-sized schools reported for some of the other adult coastal pelagic clupeids (Juhl 1966, Bullis et al. 1971). Further examination may be warranted to determine how variations in distributional patterns affect the stability of yearly recruitment for these species.

We found no *H. jaguana* larvae less than 4.0 mm SL beyond the 51-m isobath, which is consistent with Houde's (1977b) finding of no *H. jaguana* eggs beyond 85 km from the shore of west Florida. However, some adults move offshore during winter (Gunter 1945, Springer and Woodburn 1960, Roessler 1970, Perret et al. 1971, Swingle 1971, Christmas and Waller 1973), and we did find larvae (7–14 mm SL) in springtime waters of the open Gulf, which may suggest some spawning in this offshore population. If we assume that a 13.7-mm SL specimen captured 16 April had a growth rate of 0.8–1.0 mm/day (Detwyler and Houde 1970, Saksena and Houde 1972) and a hatching size of 2.5 mm,

then the earliest probable spawning offshore was the first week of April.

In this study, salinity values averaged less than 32 ppt at capture sites for all sizes of *H. jaguana* larvae collected (1982 = 31.8 ppt; 1983 = 26.3 ppt) and also for recently hatched larvae (1982 = 30.4 ppt; 1983 = 22.8 ppt) captured across the northern Gulf. Previous studies, primarily from high-salinity areas off west Florida (Houde 1977b, Collins and Finucane 1984) and Texas (Compton 1964), found *H. jaguana* larvae in waters of 32 ppt or above.

Similarly, in this gulfwide study, recently hatched larvae (<4.0 mm SL) of *O. oglinum* were often collected in waters with salinities below 30 ppt, though spawning in Florida waters has been reported only at salinities of 32.4–38.4 ppt (Fuss 1968, Fuss et al. 1969, Fuss and Kelly 1970, Houde 1977c, Collins and Finucane 1984).

Opisthonema oglinum larvae were, in 1982, the most abundant clupeid examined, which helps support claims that the adults are between the first and third most abundant coastal pelagic in the Gulf (Bullis and Carpenter 1968, Bullis et al. 1971, Juhl 1976). In 1983, however, larval abundance decreased relative to the other clupeids, and *O. oglinum* were far from being the most abundant larval clupeid. The greatest single-station concentration and highest overall abundances of *O. oglinum* larvae were found off Louisiana and eastern Texas, though the adults are reportedly more abundant off west Florida than in the north-central Gulf (Juhl 1966, Bullis and Thompson 1967, Klima 1971). Our findings did, however, support the claim that larval *O. oglinum* abundance off west Florida is second only to that of *S. aurita* (Houde et al. 1979). Also, larval *O. oglinum* abundances peaked in June, the month of maximum spawning for this species in both the eastern and northern Gulf (Fuss 1968, Fuss et al. 1969, Fuss and Kelly 1970, Ditty 1986).

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Other scientific names recently used: *E. acuminatus* and *E. sadina* (Whitehead 1963, 1973).

Adult Distribution

Geographic

Bay of Fundy southward to Cape Canaveral, Florida (Hildebrand 1964), and east and north coasts of Gulf of Mexico, Cuba, Colombia, Venezuela, Trinidad, Guiana, and French Guiana (Whitehead 1973, Fischer 1978); Pacific United States, Galapagos Islands, northcentral Pacific near Hawaii, Japan, south and west coasts of Australia (Jones et al. 1978); east Mediterranean and Red Sea (Jones et al. 1978); South Africa (Whitehead 1963).

Vertical (depth) or distance from shore

Probable planktonic feeder; forms dense schools, mainly in deep waters along the continental shelf and slope or deeper (Bullis et al. 1971, Klima 1971, Reintjes 1979a, Crawford 1981–South Africa), but concentrates between 37 and 92 m (Bullis et al. 1971, Klima 1971); rarely taken nearshore (Bullis et al. 1971, Reintjes 1980).

Adults taken over the southeast U.S. continental shelf in bottom trawls between 10 and 366 m; apparent seasonal shift in depth distribution—distribution more offshore (56–183 m) during summer–fall and more inshore (10–27 m) during winter–spring (Barans and Burrell 1976).

Apparently does not migrate great distances horizontally (Reintjes 1979a).

Undergoes diurnal vertical migration—found at surface at night and 9–37 m off the bottom during the day (Bullis et al. 1971).

Tends to school with other species such as Spanish sardine *Sardinella aurita* (Bullis et al. 1971), and rough scad *Trachurus lathami* (Reintjes 1979a); juveniles school with chub mackerel *Scomber japonicus* (Reintjes 1979b, Crawford 1981).

Stock Abundance

Gulf of Mexico

Gulf Exploratory fishing by RV *Oregon* and *Oregon II* caught round herring from Florida to Texas; *Oregon II* cruise in January 1969 reported an exceptionally large school of round herring and rough scad 56 km long off Cameron, Louisiana (Reintjes 1979a). Adults caught regularly in midwater and bottom trawls (Reintjes 1979a).

Eastern Gulf Abundance of eggs and larvae at station depths 55–183 m indicates large biomass of adults (Houde 1973). Biomass estimates based on two seasons of egg and larval fish surveys (1971–72 and 1972–73) ranged from 131,136 to 717,815 metric tons (t); best estimate of mean potential annual yield of stock, 50,000–250,000 t, the equivalent of a potential harvestable yield of 6.5–32.7 kg/ha of round herring habitat at the 30–200 m depth zone (Houde 1977a).

Tampa, Florida Mixed school of round herring and Spanish sardine 80 km west of Tampa, 80 km long, 16 km wide, and about 3.7 m thick (Bullis et al. 1971).

Other

Atlantic coast Phenomenal occurrences observed in some years (Scattergood 1953, Hildebrand 1964).

South Africa Exceptionally large patch of round herring stretching discontinuously for over 80 km, seen the night of 18 June 1973 (Crawford 1981).

Gulf of California Larvae of this potentially important commercial species were the eleventh-most abundant (Moser et al. 1974).

Fisheries

Gulf of Mexico

Other

Japan Supports a commercially important purse-seine fishery (Hara 1977).

Southeastern Atlantic Reported to be one of the most important fishes off Cape Peninsula of the Republic of South Africa (O'Toole and King 1974).

South Africa Supports a small but valuable and fairly regular purse-seine fishery; annual catches of 10,000–35,000 t (Crawford 1981).

Problems

Gulf Not readily taken by purse-seining gear; would require new and innovative harvesting techniques (Juhl 1976).

South Africa Its large scales reported to clog purse-seining nets, necessitating extensive net cleaning; fishermen therefore sometimes avoid setting on these schools when other species are present (Crawford 1981).

Reproduction

Sexual maturity

Eastern Gulf Of 65 specimens (93–163 mm SL) collected in August and November 1974, specimens >100 mm SL ($N=59$) were mature or near ripe; six additional females (157–160 mm SL) collected off east Florida in June 1973 were spent (Houde 1977a).

South Africa For *E. micropus*, 50% of fish mature at age-3 ($\bar{x}$ length 202 mm SL) and 100% at age-5 (Geldenhuys 1978).

Japan For *E. micropus*, length at first maturity 170 mm SL (Ito 1968).

Sex ratio

Eastern Gulf Sex ratio not significantly different from 1:1, based on 71 adults examined, 1.22M:1F (Houde 1977a).

South Africa For *E. micropus*, ratio of approximately 1M:1.2F during 1965–71 (Geldenhuys 1978).

Fecundity

Eastern Gulf Based on eight females measuring 130–165 mm SL, fecundity of 7446–19,699 eggs (equivalent to 150–428 ova/g, $\bar{x}$ 296.5) (Houde 1977a).

Spawning season

Gulf Spawning season December–May (Houde and Fore 1973).

Eastern Gulf Nighttime spawning, based on collections of early embryonic stages; peak spawning estimated to occur at 2200 EST (Houde 1977a); evening spawning in Hawaii (Watson and Leis 1974). Commonly spawns at depths >37 m in November and February, and rarely in May; abundance of eggs and larvae at station depths of 55–183 m indicates large biomass of adults (Houde 1973). Spawns mostly in depths 30–200 m and deeper from mid-October to the end of May; peak spawning in January–February; no eggs and larvae collected June–September; eggs collected at surface temperatures of 18.4°–26.9°C and salinities of 34.5–36.5 ppt; larvae <5.0 mm SL collected at surface temperatures of 20.5°–26.9°C and salinities of 34.1–36.8 ppt (Houde 1977a).

Western Gulf Spawning December–early March 54–197 km off east Texas and Louisiana; most eggs collected over depths of 27–100 m, possibly some spawning off the continental shelf (Fore 1971).

Off Caminada Pass, Louisiana In an ichthyoplankton survey November 1981–October 1982, larvae taken in January and February (Ditty 1986).

Louisiana Between the Mississippi and Atchafalaya river deltas, larvae collected during a January–February 1976 survey between 10 and 100 m; 99% of the round herring taken outside of the 30-m contour (Ditty and Truesdale 1984).

South Texas Eggs and larval fish collected December–April between 30 and 180 m, the depth limits of sampling (Finucane et al. 1979).

U.S. South Atlantic Bight Larvae collected in January and February (Fahay 1975).

Gulf of California Most abundant in April; larvae taken in waters 19.7°–23.5°C (Moser et al. 1974).

Hawaii Spawns October–July, peaking in late April, in waters 21.5°–26.5°C and 30.5–36.6 ppt (Watson and Leis 1974).

South Africa Spring–summer spawner (conditions equivalent to fall–winter in the northern hemisphere) (Crawford 1981).

Eggs

General description

South Africa Eggs smooth, spherical, buoyant, with large, lightly segmented yolk (O'Toole and King 1974).

Japan Pelagic eggs, transparent, yolk pale-yellow with fine, bubblelike structures (Uchida et al. 1958, *E. micropus*).

Egg diameter

Gulf Fertilized egg diameter, 1.17–1.37 mm ($\bar{x}$ 1.29 mm) (Houde and Fore 1973).

South Africa Egg diameter, 1.32–1.47 mm ($\bar{x}$ 1.37 mm; $N=160$) (O'Toole and King 1974).

Perivitelline space

Gulf Narrow perivitelline space, 10% of egg diameter ($\sim$ 0.12–0.14 mm) (Houde and Fore 1973).

South Africa Narrow perivitelline space, 0.12–0.16 mm (O'Toole and King 1974).

Hawaii Narrow perivitelline space (Watson and Leis 1974).

Oil globule

Gulf None (Houde and Fore 1973).

South Africa None (O'Toole and King 1974).

General review of clupeiformes, none (McGowan and Berry 1984).

Incubation time

Gulf About 2.1 days at 21°–22°C (Houde 1977a).

Hawaii Approximately 2 days at surface temperatures of 23°–25°C (Watson and Leis 1974).

South Africa At 11.0°C, 135 h; at 20.5°C, 36 h (O'Toole and King 1974).

Larvae

Hatching length

Western North Atlantic Total lengths of 3.8–4.8 mm, eyes unpigmented (Fahay 1983).

South Africa Total lengths of 3.85–4.50 mm (live), 3.75–4.00 mm (preserved) (O'Toole and King 1974); egg diameters slightly larger than those reported by Houde and Fore (1973) for the Gulf of Mexico.

Japan *E. micropus*, 3.8 mm (Uchida et al. 1958); 4.84 mm (Mito 1961).

Early-life-history information

Eastern Gulf Greater numbers caught at night (daytime net avoidance); larvae 13.0–18.0 mm apparently able to avoid nets at night as well, i.e., day:night ratio approaches one (Houde 1977a).

Eastern Gulf Houde (1977a) calculated:

a) Mortality estimates for the 31-day period between spawning and the 15.5-mm larval stage of 99.4% for a 1971–72 survey and of 98.3% for a 1972–73 survey

b) Probable daily larval growth increment of 0.3–0.7 mm (equivalent to an instantaneous growth coefficient of 0.03–0.07)

c) Probable ranges of instantaneous mortality coefficients (z) of 0.09–0.17 in the 1971–72 survey and 0.08–0.17 in the 1972–73 survey

d) Most probable instantaneous mortality coefficients per millimeter increase in length of 0.23 for 1971–72 and 0.37 for 1972–73 (a percentage loss per millimeter increase in length of 20.3% and 30.5%, respectively)

e) Most probable daily mortality estimates of 0.132 in 1971–72, a 12.3% loss per day, and 0.129 in 1972–73, a 12.1% loss per day.

Meristics

Myomeres 48–50, postdorsal-preanal myomeres 3–4 (Houde and Fore 1973, eastern Gulf); total vertebrae 48–56, precaudal 15–17, caudal 32–34 (Jones et al. 1978, northwestern Atlantic); 53–55 (Miller and Lea 1972, California); 48–50 myomeres by 5.0-mm notochord length (NL), 52–53

by 18.7–24.0 mm (O'Toole and King 1974, South Africa); 48–50 (Wongratana 1980, Indo-Pacific).

Dorsal fin rays 18–21 for larvae >15 mm TL (Houde and Fore 1973); 16–22 (Jones et al. 1978); 18–22 (Wongratana 1980); 18–20 (Miller and Lea 1972).

Anal fin rays 11–12 (Houde and Fore 1973); 9–13 (Jones et al. 1978); 10–19 (Wongratana 1980, Miller and Lea 1972).

Pelvic fin rays 8 (Jones et al. 1978); 8–9 (Wongratana 1980).

Pectoral fin rays 14–17 (Jones et al. 1978).

Larval descriptions

Gulf Egg and larval illustrations, comparative information, and larval key based on literature review and laboratory-reared and wild-caught larvae (Houde and Fore 1973).

Northwestern Atlantic Excellent atlas of egg, larval and juvenile stages (Jones et al. 1978).

Western Atlantic Illustrations of postlarvae collected off Florida (Hildebrand 1964).

South Africa Egg and larval illustrations from wild-caught eggs hatched in the laboratory (O'Toole and King 1974).

Hawaiian Islands Illustrations of both laboratory-reared and wild-caught larvae and additional early-life-history information from the literature (Miller et al. 1979).

Hawaii *E. micropus* (Watson and Leis 1974).

Australia Illustrations of wild-caught eggs and larvae (Blackburn 1941).

Japan *E. micropus* (Uchida et al. 1958, Mito 1961).

Juvenile

Western Atlantic Minimum juvenile size, 28.0–33.0 mm TL (Hildebrand 1964).

Gulf Juveniles not usually taken in estuaries (Springer and Woodburn 1960).

Other scientific names recently used: *H. majorina* (Fischer 1978) and *H. pensacolatae* (Whitehead 1973).

Adult Distribution

Geographic

Western Atlantic Distributed from New Jersey (Berry 1964, Fischer 1978) to southern Brazil (Reintjes 1979a), including the Gulf of Mexico (Klima 1971, Martinez 1972); extremely rare north of Cape Hatteras, North Carolina, and not abundant north of Cape Canaveral, Florida (Reintjes 1979a); abundant and widely distributed in Caribbean-Mexican waters and from Cape Canaveral to Brazil (Gorbunova and Zvyagina 1976).

Two similar species, *H. clupeiola* and *H. humeralis* (= *H. callolepis*, Whitehead 1973), occur in southern Florida, the Caribbean Islands, and along the South American coast, but *H. clupeiola* is rare in the northern Gulf (Reintjes 1979a).

Vertical (depth) or distance from shore

Gulf Abundant in nearshore estuaries and bays spring-fall, evidently moves offshore in winter (Gunter 1945, Springer and Woodburn 1960, Roessler 1970, Perret et al. 1971, Swingle 1971, Christmas and Waller 1973).

Northeastern Gulf Abundant plankton predator (not a filter feeder; Reintjes 1979a), schools near surface along coasts, usually within the 37-m depth contour (Klima 1971); a near-shore species, based on the distribution of eggs and larvae—adult populations may occur within 5.6 km of the west Florida coast (Houde 1977b).

Found schooling with Spanish sardine and Atlantic thread herring (Low 1973).

Stock Abundance

Gulf of Mexico

Gulf Abundant (Briggs 1958, Rivas 1963, Berry 1964, Fischer 1978). “The most common inshore clupeid on the continental shelf, except where it is replaced inshore off Louisiana by the menhaden [*Brevoortia patronus*]” (Hoese and Moore 1977:135). Species accounts for approximately one-third of fish discarded by the shrimp fishery (Reintjes 1980).

Eastern Gulf Estimates of mean biomass from 3 years (1971–73) of annual spawning stock range between 184,182 and 265,000 t; potential yield from the eastern Gulf, based on the 3-year biomass estimate, 46,132–92,264 t or 7.7–15.4 kg/ha (Houde 1977b).

Northeastern Gulf The most common clupeid (Springer and Woodburn 1960, Low 1973).

Horn Island, Mississippi The numerically dominant resident species 1975–77 (Modde 1980, Modde and Ross 1981).

Galveston, Texas The most abundant clupeid late summer–early fall (Arnold et al. 1960).

Other

No species-specific information found.

Fisheries

Gulf of Mexico

Gulf and Caribbean Because of its abundance, an important latent fishery resource (Reintjes and June 1961, Bullis and Thompson 1970, Klima 1971, Houde et al. 1974, Houde 1977b).

Florida Small commercial and recreational bait fishery (Klima 1959, 1971; Martinez and Houde 1975; Fischer 1978); catch not reported, probably less than 454 t annually (Houde 1977b).

Other

West Indies Caught for human consumption (Rivas 1963, Martinez and Houde 1975); sold fresh and canned in Cuba and Venezuela (Rivas 1963, Klima 1971, Martinez and Houde 1975, Fischer 1978).

Cuba, Brazil, and the Dominican Republic Small catches recorded by FAO (Houde 1977b); in 1975 a combined *Harengula* spp. catch totaling 1725 t taken off Cuba and the Dominican Republic (Fischer 1978).

Brazil Clupeids are the most important fishery resource; *Harengula* spp. ranked third behind the Brazilian sardine *Sardinella brasiliensis* and *Opisthonema oglinum* (Hubold and Mazzetti 1981).

Problems

Species known to be important forage for predatory fish like Spanish mackerel *Scomberomorus maculatus* (Klima 1959), and snappers, Lutjanidae (Martinez 1972, Martinez and Houde 1975).

Species an important prey item for king mackerel *Scomberomorus cavalla* (Beaumariage 1973); mangrove (gray) snapper *Lutjanus griseus* (Roessler 1967); bluefish *Pomatomus saltatrix*; red drum *Sciaenops ocellatus*; sea trout *Cynoscion* spp.; snook *Centropomus* spp.; and tarpon *Megalops atlanticus* (Reintjes 1979a).

Relatively small school size, <0.9–1.8 t, in inshore waters; schools associated with grass beds (Low 1973).

Reproduction

Sexual maturity

Florida Mature at age-1 (80–130 mm) (Martinez and Houde 1975); probably attains lengths of 100–130 mm by age-1 (Roessler 1970).

East Florida Size at first maturity 78–85 mm SL; most mature by age-1 and all by age-2 (Martinez 1972).

Sex ratio

Gulf Sex ratio ~1:1 (Reintjes 1979a).

East Florida Sex ratio 1M:1.1F (Martinez and Houde 1975).

Fecundity

Florida On the basis of 22 specimens (85–163 mm SL), fecundity estimated to be 5563–52,753 ova, and relative fecundity to be 323–807 ova/g ($\bar{x}$ 548 ova/g) (Martinez 1972).

East Florida Female ovaries contained three modes of oocytes, two of which were spawned during one spawning season (Martinez and Houde 1975).

Spawning season

Some evidence of intermittent or spasmodic spawning (Gunter 1945, 1958; Martinez 1972; Christmas and Waller 1973; Modde 1980).

Two spawning peaks or waves of recruitment suggested (Gunter 1945, 1958; Springer and Woodburn 1960; Modde 1980).

Northeastern Gulf Newly fertilized eggs collected only at night (Houde 1977b); estimated peak spawning time 2200 h (Houde and Palko 1970, Houde et al. 1974). Based on cruise collections 1971–74, species found to spawn January–September with peak activity May–August; earliest spawning (January–March) confined to southern Florida. Spawns along the coast, mostly in waters <20 m deep (no eggs collected in waters deeper than 27 m) and mostly within 50 km of the coast (none >85 km from the coast). Eggs collected at surface temperatures of 20.8°–30.7°C and salinities of 29.9–36.9 ppt; 82% of eggs in surface temperatures >24°C, and 71% in salinities >35 ppt. Larvae ≤5 mm SL (≤5 days old) taken at surface temperatures of 18.4°–30.5°C and salinities of 27.3–36.9 ppt; 71% of these taken from stations with surface temperatures >24°C, and 62% from waters with salinities >35 ppt (Houde 1977b).

East Florida Based on gonadal indices, possibly an intermittent spawner; spawning season February–August with April–May peak (Martinez 1972).

Biscayne Bay, Florida Based on gonadal indices, spawns late March–May (Low 1973).

South Florida Larvae taken in March and April; on 15 March 1966, ripe females taken 40 km north-northeast of Key West (Turner 1969).

Everglades, south Florida Probably spawns in winter and spring; smallest specimens (25 mm) collected in January and February (Roessler 1970).

Everglades, southwest Florida During quarterly sampling of coastal and estuarine waters, 243 larvae taken in temperatures of 20.1°–30.0°C and salinities of 32.0–38.0 ppt; most abundant during May (collected larvae 1.9–20 mm SL) and August (9.5–30 mm SL) in coastal waters 5.5–9.0 m deep, also taken in February (10–16 mm SL); no larvae collected in November or in estuarine waters (Collins and Finucane 1984).

West Florida Eggs collected very close to shore March–August (Houde 1973).

Alabama estuaries Spawning in April–May (Swingle 1971).

Lower Mobile Bay, Alabama Larvae collected primarily at the surface April–May (Williams 1983).

Mississippi Spasmodic spawning spring–late summer; fish <25 mm TL collected May, July, August, and September (peak in July) (Christmas and Waller 1973). Off barrier islands, July surface tows collected larvae 10.0–14.0 mm SL (Stuck and Perry 1982).

Barataria and Timbalier Bays, Louisiana Took 330 specimens (3.3–5.5 mm) in July and August (Walker 1978).

Off Caminada Pass, Louisiana Collected 5339 specimens ranging 14–33 mm SL ($\bar{x}$ 19.4 mm) May–September (peak in July), suggesting an April–August spawning season in southeast Louisiana (Sabins 1973). An ichthyoplankton survey November 1981–October 1982 collected larvae April–October with a peak abundance July–August; scaled sardine larvae represented 8% of all clupeid larvae taken; 80% of larvae taken in surface water temperatures >25°C; most larvae (79%) taken near surface, 19% taken at mid-depth, and only 2% collected near bottom (Ditty 1986).

Texas Larvae 2.5–10.0 mm collected off the coast May–September (Hoese 1965).

Galveston Island, Texas Larvae collected May or June to August (Arnold et al. 1960).

Aransas–Corpus Christi Bay Complex, Texas April–August, 1384 larvae taken (2.7% of the total larval catch), with peak in August (Allshouse 1983).

Port Aransas, Port Mansfield, and Port Isabel Ship Channels, Texas During 7 April–13 May 1964, 104 larvae of *Harengula* sp. taken in temperatures of 19.5°–26.4°C and salinities of 34.5–36.7 ppt; one 7-mm larva taken at Port Isabel on 17 September in 27.3°C and 36.0 ppt (Compton 1964).

Brazil Spawns within 18.5 km of coast and within the 65-m depth contour; spawning area temperatures (measured at 10-m depth) were 19.2°–27.0°C and salinities 34.86–35.85 ppt (Matsuura 1972).

Southwest Atlantic In sampling between 25°S and 40°S off Brazil and Argentina, three eggs collected at the 20-m isobath and 21 larvae taken in depths of 20–62 m; at 10-m depth, temperatures at positive stations were 16.5°–23.3°C and salinities 33.8–35.4 ppt (Hubold and Ehrlich 1981).

Eggs

General description

Pelagic eggs (Houde and Palko 1970, lab. study).

Gulf Embryo and yolk occupy about one-half of the egg capsule (Houde and Fore 1973).

Caribbean–Mexican waters Eggs transparent and spherical, yolk consisting of large, clearly discernible granules; yolk diameter 0.80–0.85 mm; external membrane thin and colorless (Gorbunova and Zvyagina 1976).

Egg diameter

Caribbean–Mexican waters Fertilized eggs have diameters of 1.35–1.98 mm, mature ova diameters 0.67–0.95 mm (Gorbunova and Zvyagina 1976).

Gulf Average egg diameter 1.55–1.85 mm, $\bar{x}$ 1.66 mm (Houde and Fore 1973). Average egg diameter 1.76 mm (Houde and Palko 1970, lab. study).

Mean egg diameter (2 h after fertilization) 1.638 mm (1.48–1.72 mm) in artificially fertilized eggs (Matsuura 1972).

Western North Atlantic Egg diameters 1.55–2.00 mm (Fahay 1983).

Perivitelline space

Gulf Wide, ~50% of egg diameter (Houde and Fore 1973).

Caribbean–Mexican waters Large space, 40%–50% of total egg diameter (Gorbunova and Zvyagina 1976).

Very wide, $\bar{x}$ width 0.90 mm (Matsuura 1972, artificially fertilized eggs).

Oil globule

Single small oil globule, average diameter 0.08 mm (Houde and Palko 1970, lab. study).

Single whitish-yellow oil globule, $\bar{x}$ diameter 0.089 mm (0.071–0.101 mm) in artificially fertilized eggs (Matsuura 1972).

Gulf Single light yellow oil globule, diameter 0.07–0.10 mm, $\bar{x}$ 0.09 mm (Houde and Fore 1973).

Caribbean–Mexican waters Single oil droplet, diameter 0.07–0.1 mm (Gorbunova and Zvyagina 1976).

Incubation time

West Florida Less than 24 h in temperatures >24°C, mean duration of egg stage ~0.8 day (Houde 1977b).

Caribbean–Mexican waters Approximately 24 h in temperatures 23°–28°C (Gorbunova and Zvyagina 1976).

Larvae

Hatching length

Hatching length 2.4 mm, but increases to >4.0 mm within 15 h (Houde 1977b).

Hatching length 2.85–2.97 mm (Gorbunova and Zvyagina 1976).

Early-life-history information

Larvae photopositive throughout larval stage, began feeding at 4.0–5.0 mm TL (Houde and Palko 1970, lab. study).

West Florida No larvae >18.0 mm long taken during daylight tows; no apparent relationship between abundance of either eggs or larvae and zooplankton volumes in specimens collected in 333- μ m mesh bongo nets during 1972–74 (Houde 1977b). Houde (1977b) calculated:

a) Apparent mortality of 85%–91% between spawning and hatching; <2% survived to 5.5 mm (after two days feeding); >99.9% mortality occurred by 15.5 mm

b) A most probable mortality estimate for data on abundance at age of $z = 0.283 \pm 0.075$ ($\pm 95\%$ confidence level), with a range of 0.182–0.347, which corresponds to a daily loss rate of 24.7% (range of 16.7%–29.3%); mortality coefficient of 0.246 for fully vulnerable larvae, 3.1–20.0 mm (equivalent to a daily loss rate of 21.8%)

c) An instantaneous rate of daily decline in abundance per millimeter increase in length for larvae 3.1–20.0 mm SL (provided gear avoidance was not too significant) of 0.383 ± 0.083 ($\pm 95\%$ confidence limit), which is equivalent to a 31.8% decrease in larval abundance per 1-mm increase in length.

Caminada Pass, Louisiana Twice as many larvae caught during the day as during the night (Sabins 1973).

Daily growth rates of larvae reared on low and high food ration 0.80–0.81 mm/day (Saksena and Houde 1972).

Mean daily growth increments of 0.06 mm/day for larvae reared at 21°–23°C, 1.04 mm/day for those reared at 32°C; larvae survived best at 26°–32°C, critical low and high temperatures for larval survival, 20°C and 35°C (Saksena et al. 1972).

Most probable growth rate, instantaneous growth coefficient (g) of 0.09 (Houde 1977b).

Mean growth from hatching through 25 days old, 1 mm/day; after metamorphosis (25–30 mm TL), mean growth 0.7 mm/day; after 100 days larvae averaged 76 mm TL (Houde and Palko 1970, lab. study).

Growth rate 4th–17th day after hatching 1.0 mm/day (Detwyler and Houde 1970, lab. study).

Larvae 18–20 days old, 20 mm long (Gorbunova and Zvyagina 1976, lab. study).

Growth rate of postlarvae and juveniles, 9–10 mm/mo (Low 1973, Florida); 11–13 mm/mo (Christmas and Waller 1973, Mississippi); 12.5 mm/mo (Gunter 1945, Texas).

Meristics

Myomeres 40–42, postdorsal-preanal myomeres 5–7 (Houde and Fore 1973, eastern Gulf); vertebrae 41–43 (Whitehead 1973, Guianas).

Dorsal fin rays 15–18, usually 16–17 (Boschung 1957, Alabama); 17–19 (Houde and Fore 1973); 17–18 (Whitehead 1973).

Anal fin rays 17–18 (Boschung 1957, rarely 16; Houde and Fore 1973; Whitehead 1973).

Larval descriptions

Gulf Egg and larval illustrations, comparative information, and larval key based on literature review and lab-reared and wild-caught larvae (Houde and Fore 1973).

Southeast Florida Egg and larval illustrations, comparative information from collected eggs reared in the lab (Houde et al. 1974).

Egg and larval illustrations from artificially fertilized eggs reared in the lab (Gorbunova and Zvyagina 1976).

Brazil Egg and larval illustrations and descriptions from artificially fertilized eggs (Matsuura 1972).

Japan *H. zunasi* (Uchida et al. 1958, Takita 1966).

Juvenile

Florida Larvae undergo metamorphosis at 22–24 mm SL (Reintjes 1979a); or at 25–30 mm TL, 25 days after hatching (Houde and Palko 1970). Age-1 fish averaged 106.6 mm SL and 29.9 g in weight (based on 10 females); age-2 averaged 136.6 mm SL and 69.7 g (based on 5 females) (Martinez 1972).

South Florida Age-1 fish, 100–130 mm long (Roessler 1970).

Cedar Key, Florida Four specimens (24–31 mm) caught November in water 20.8°C and 22.8 ppt (Reid 1954).

Everglades, Florida Most fish (94% of 23,283 specimens) caught May (modal lengths 35–65 mm) to November (55–65 mm), smallest fish (25 mm) taken in January and February; fish caught in waters 15.5°–34.4°C and 15.5–45.2 ppt (Roessler 1970).

West Florida Two fish (34 and 64 mm) taken October in water 25°C and 30.2 ppt, and two fish (115 and 125 mm) taken April in water 25°C and 20.8 ppt (Kilby 1955).

Tampa Bay, Florida Species not common January–April; only one specimen taken in salinities <25 ppt (Springer and Woodburn 1960).

Alabama June to November, 162 specimens taken from estuaries; smallest fish (20 mm TL) taken in August; several thousand small juveniles taken June and July 1969 on Dauphin Island's Gulf beach (Swingle 1971).

Mississippi Total of 2416 fish (23–158 mm TL) taken all months except January, March, and November (99% of total catch taken June–October, 1102 fish taken October alone), fish collected in waters 5.0°–34.9°C and 0.0–35.5 ppt (only 15 fish taken in salinities <20 ppt, majority taken 30–35.5 ppt) (Christmas and Waller 1973). Off barrier islands, juveniles (21–30 mm SL) taken in July surface tows (Stuck and Perry 1982).

Horn Island, Mississippi Two fish (49 and 52 mm TL) taken in August and three fish (62–85 mm TL) in November; fish collected in waters 18.7°–31.0°C and 17.1–28.3 ppt (Franks 1970). Fish collected between April (16–25 mm) and August (21–25 mm); modal length interval in June, 31–35 mm (Modde 1980). Smallest fish (<29.0 mm) taken August and September, fish 30–50 mm or smaller collected in waters 25°–30°C and 25–30 ppt (Perry and Boyes 1978).

Chandeleur Islands, Louisiana Total of 15 specimens (35–70 mm SL) collected July, September, and November; presence of 35-mm fish in July suggests April–May spawning (Laska 1973).

Louisiana Total of 103 specimens collected May–October in waters 10°–34.9°C and 6.7–29.9 ppt; very few fish taken in waters >15 ppt (Perret et al.1971).

Caminada Pass, Louisiana Total of 5339 fish (14–35 mm SL; $\bar{x}$ 19.4 mm) collected May–September, peak in July (Sabins 1973).

Marsh Island, Louisiana Total of 657 juveniles collected June–October in waters 23.3°–32°C; 574 specimens taken in one collection on 4 September 1971 had a mean length ($\pm$ SD) of 31.0 ± 6.2 mm (Tarbox 1974).

Galveston Island, Texas Juveniles collected September–November, larvae collected May–June to August (Arnold et al. 1960).

Mustang Island, Texas Fish collected March–July (McFarland 1963).

Texas A total of 2140 fish taken in waters 20.5°–30.5°C (only nine fish in temperatures $\leq 24.0^\circ\text{C}$) and 4.8–36.9 ppt (only 16 fish in salinities <25 ppt); small fish found in June (33 mm) and September (27 mm) (Gunter 1945, *H. macrophthalma*).

Other scientific names recently used: *O. captivai* (Fischer 1978).

Adult Distribution

Geographic

Gulf of Maine (Cape Cod) to Santa Catarina, Brazil (Fischer 1978, Reintjes 1979a); also Bermuda (Jones et al. 1978); West Indies (Hildebrand 1964); and throughout the Gulf of Mexico (Fischer 1978).

Western North Atlantic Two species of *Opisthonema* occur (Richards et al. 1974).

Vertical (depth) or distance from shore

A migratory, coastal, surface-schooling species (Klima 1971, Jones et al. 1978); one of the larger marine herrings, reaching 305 mm and 340 g (Reintjes 1979a); filter feeds primarily on zooplankton (Hildebrand 1964, Low 1973). Appears to move south during fall and winter when temperatures fall below 20°C and to concentrate within 10–16 km of shore; appears to move northward and disperse offshore with warming temperatures in spring (Fuss et al. 1969, Kinnear and Fuss 1971, Houde 1973, Reintjes 1979a).

Prefers summer temperatures of 26°–29°C, absent at temperatures <17°C or >29°C; prefers salinities of 32–34 ppt (Fuss et al. 1969, Kinnear and Fuss 1971).

Prefers depths below 35 m (Klima 1971); seldom at depths >18 m and usually in depths <11 m, frequently in upper 3 m (Kinnear and Fuss 1971).

Schools with Spanish sardine (Springer 1957); scaled sardine (Fuss et al. 1969, Low 1973); and round scad, *Decapterus punctatus* (Houde et al. 1984).

Stock Abundance

Gulf of Mexico

Gulf Second most abundant species behind the anchovies and ahead of gulf menhaden, *Brevoortia patronus* (Bullis and Carpenter 1968, Bullis et al. 1971). Most abundant coastal pelagic; estimated latent potential 907 million kg with greatest abundance off Florida; biomass estimated to be greater than 3.6 billion kg (Juhl 1976).

West Florida The dominant species, occurs in schools of 2–9 t; 12–14 surface schools observed at once, usually in depths <18 m (Juhl 1966); resource along Florida possibly as much as 680,400 t (Kinnear and Fuss 1971).

Eastern Gulf Annual catch possibly as great as 453,600 t (Sykes 1968). Estimated adult biomass (standing stock) of 108,000–372,000 t, based on egg and larval fish surveys in 1971–73 (Houde 1973, Houde 1977c); best estimate of annual potential yield 60,300–120,600 t (Houde 1977c).

Northeastern Gulf Estimated stock of ~907,200 t, estimated density of one school per 2.6 km²; appears more often in collections and seen probably more often than all other surface schooling species combined (Bullis and Thompson 1967).

Caminada Pass, Louisiana Third most abundant taxa of larvae collected between November 1981 and October 1982; represented 58% of all clupeid larvae and 9% of the total number of larvae taken during entire study (Ditty 1986).

Northern Gulf Not as abundant as off west Florida (Bullis and Thompson 1967, Klima 1971), but surface schools abundant during summer and subsurface schools present during remainder of the year (Bullis and Thompson 1967).

Probably no exchange between the Atlantic and Gulf; fish tagged in the Atlantic never recovered in the Gulf (Reintjes 1980).

Other

No species-specific information found.

Fisheries

Gulf of Mexico

Gulf Possibly represents an unexploited fishery (Hoese and Moore 1977). Finucane and Vaught (1986) reviewed the historical Gulf fishery and potential uses for this species.

West Florida Experimental sardine canning investigated (E.J. Conrad, Jr., Port Clyde Foods, Inc., P.O. Box 528, Rockland, ME 04841, pers. commun., Aug 1985).

West-central Atlantic Possibly the largest single unexploited species (Bullis et al. 1971).

Western Atlantic Total catch of 12,016 t in 1974; 2434 t landed in the United States (Houde 1977c).

Florida Moderate amounts harvested along the Atlantic coast, off Fernandina Beach, Florida, and off Fort Myers in the Gulf by menhaden fishermen may indicate commercial potential (Klima 1971).

Charlotte Harbor, west Florida Atlantic thread herring described as having (1) a protein content of 65–68% (gulf menhaden usually guarantees 60%), (2) a fish-meal yield higher than gulf menhaden (i.e., ratio of meal to fish about 1:4 as compared with 1:5), (3) a meal of finer texture, and

(4) an oil yield during the summer of 3785 L/million fish, which increased during the winter to 12,490 L/million fish (gulf menhaden generally yield over 37,850 L/million fish) (Fuss et al. 1969).

Could stabilize production in the fish-reduction industry by making the production period year-round because Atlantic thread herring are present in many coastal waters when gulf menhaden are not (Butler 1961).

Readily taken by purse-seine gear (Juhl 1976), although harder to catch than gulf menhaden and generally not available on menhaden grounds (Kinneer and Fuss 1971).

Potential for large aggregate catches with *Sardinella aurita* and *Decapterus punctatus*, perhaps as large as 1 million–2 million t in the eastern Gulf (Houde 1975, 1977a,b,c; Reintjes 1979a, 1980).

Small seasonal fishery for bait, food for cats, and the aquarium trade, about 454–1,814 t annually (Houde et al. 1984).

Other

Southeastern Atlantic Some potential for expansion of existing fishery (Pristas and Cheek 1973).

South Brazil Clupeids the most important fishery resource; *O. oglinum* second in importance behind *Sardinella brasiliensis* (Hubold and Mazzetti 1981).

Caribbean Small commercial production throughout Caribbean (Bullis and Carpenter 1968, Bullis et al. 1971).

Gulf of Mexico and Caribbean Marketed fresh, frozen, and salted, and used in the fish meal industry. FAO statistics for 1975 indicate a total catch for the Gulf of Mexico and Caribbean of 5714 t (Venezuela, 1900 t; United States, 3104 t; Cuba, 600 t; Dominican Republic, 110 t; USSR, negligible quantities) (Fischer 1978).

Problems

Three attempts since 1959 to industrialize Atlantic thread herring have failed (Bullis and Carpenter 1968).

Charlotte Harbor, Florida Legal problems concerning the taking of “food fish” by purse seines in 1967 (Bullis and Carpenter 1968, Fuss et al. 1969); fishery consisted of a 36-t/h plant, two small single-boat seiners, and later three gulf menhaden boats, which produced 270–450 t/day and 4536 t in the final few weeks of the fishery (Bullis and Carpenter 1968).

Prospects for a commercial fishery are discouraging because of legislation prohibiting the use of purse seines in state waters and because the species is not abundant outside state waters (Kinneer and Fuss 1971).

Species near the base of the food chain and therefore an important forage fish for all pelagic carnivores such as king and Spanish mackerel; bluefish; seatrouts; red drum; snook;

tunas *Thunnus* spp.; wahoo *Acanthocybium solanderi*; dolphin *Coryphaena* spp.; and amberjack *Seriola dumerili* (Reintjes 1979a).

Species enters the purse-seine fishery at age-1 at 100 mm or larger (Reintjes 1979a), before it is sexually mature (see below).

Reproduction

Sexual maturity

Gulf Females mature at 135–169 mm FL ($\bar{x}$ 151 mm) which can be age-1, -2, or -3; about 50% of the females mature at $\sim$ 147 mm FL, $\sim$ 1.4 yr-old (Reintjes 1979a).

West Florida Mature females 140–165 mm FL (Fuss 1968).

Sex ratio

St. Petersburg, Florida Sex ratio changes with season in nearshore Gulf, but females almost always more numerous; summer ratio 1M:5F; winter ratio 1M:1F (Fuss 1968).

Eastern Gulf Ratio indicates that males predominate in all months; 1981 ratio 1.62M:1F; 1982 ratio 1.75M:1F (Houde et al. 1984).

Fecundity

Florida Based on nine females 138–175 mm SL (53.8–109.4 g), fecundity 34,617–67,888; mean relative fecundity 594.0 ± 68 ova/g (± 2 SD), 471–746 ova/g (Martinez 1972).

West Florida Mature females had 19,000–50,000 ova (Fuss and Kelley 1970).

Eastern Gulf Based on a sample with mean weight for 48 females of 65 g, fork lengths of 135–169 mm, and mean fecundity of 30,900 eggs in the range 13,638–50,339 (Prest 1971, Houde 1973).

Spawning season

Eastern Gulf Newly fertilized eggs collected only at night (Houde 1977c). Spawning February–September with peak activity April–August; eggs primarily within 64 km of the coast but out as far as 121 km; larvae taken out to 169 km in depths of 137 m, but most collected within 88 km and within 46 m of water (Houde 1973, Houde and Fore 1973). Most spawning within the 30-m depth contour and virtually all within the 50-m contour; surface temperatures of 22.5°–30.3°C, surface salinities of 32.4–36.8 ppt (Houde 1977c); second most abundant clupeid larvae behind *Sardinella aurita* (Houde et al. 1979). Larvae taken as early as December (Turner 1969).

West Florida Based on gonadal indices, spawning March–August, peaking in May and June, when surface temperatures reach 23°–30°C and salinities 34–36 ppt (Fuss 1968, Fuss et al. 1969, Fuss and Kelly 1970).

Everglades, southwest Florida During quarterly sampling, 3568 larvae taken in temperatures of 21.1°–30.0°C and salinities of 34.8–38.4 ppt; most abundant clupeid taken, highest densities in August (2.8–43 mm SL) in coastal water depths of 5.5–8.0 m, also taken November (17–22 mm SL), February (13–14 mm SL), and May (5.0–18.0 mm SL); no larvae taken in estuarine waters (Collins and Finucane 1984).

Lower Mobile Bay, Alabama Larvae collected primarily at the surface during April and May (Williams 1983).

Barataria and Timbalier bays, Louisiana In July and August, 1335 specimens (3.3–14.4 mm) taken (Walker 1978).

Off Caminada Pass, Louisiana In an ichthyoplankton survey November 1981–October 1982, larvae collected April–October with a density peak in June and a secondary peak in September; 99% of the larvae collected in surface waters warmer than 25°C, most (62%) taken at middepth, 32% near bottom, and only 6% near surface (Ditty 1986).

Aransas–Corpus Christi Bay complex, Texas Total of 522 larvae collected April–September, with the peak in September (Allshouse 1983).

U.S. South Atlantic Bight Three larvae taken July–October (Fahay 1975).

Beaufort, North Carolina Spawning probably occurs May–June (Hildebrand 1964).

North Carolina to Venezuela Spawns March–July in the northern part of its range and possibly March–July in the southern part as well (Fischer 1978).

Puerto Rico Spawning primarily February–April (Jones et al. 1978).

Eggs

General description

Based on lab-reared specimens, eggs are pelagic, yolk mass vaguely segmented (yolk diameter 53–59% of egg diameter), chorion thin and fragile, unsculptured and unpigmented; similar to most clupeid eggs, but differs in egg diameter and oil globule from *Harengula* sp. (Richards et al. 1974), which has an egg diameter >1.50 mm and an oil globule diameter >0.10 mm (Houde et al. 1974).

Egg diameter

Gulf Egg diameter of 1.08–1.31 mm, $\bar{x}$ of 1.19 mm (Houde and Fore 1973; Richards et al. 1974, laboratory reared).

Perivitelline space

Gulf Equivalent to 33% of egg diameter (Houde and Fore 1973; Richards et al. 1974, laboratory reared).

Oil globule

Gulf Single oil globule, 0.12–0.16 mm; $\bar{x}$ 0.15 mm (Houde and Fore 1973; Richards et al. 1974, laboratory reared).

Incubation time

Less than 24 h, ~20 h at 25°–30°C (Houde 1977c).

Larvae

Hatching length

Hatching length of 3.8–4.0 mm SL; unpigmented eyes (Richards et al. 1974, laboratory reared).

Early-life-history information

Eastern Gulf Day to night ratio low, no larvae >17 mm caught during the day (Houde 1977c).

Everglades, Florida More juveniles caught on ebb tides, flood to ebb ratio 1:2 (Roessler 1970).

Charleston, South Carolina Collections with a Boothbay neuston net in July caught significantly more larvae (65 fish, 5–15 mm TL) at night than during the day (Eldridge et al. 1977).

Meristics

Myomeres 45–49, postdorsal-preanal myomeres 6–10 (Houde and Fore 1973, eastern Gulf); 46–48 (rarely 49), postdorsal-preanal myomeres for larvae <16 mm SL 8–10, and for fish <25 mm SL 5–7, predorsal myomeres 19–24, adult vertebrae total 45–49, precaudal 12–13, caudal 32–36 (Jones et al. 1978, Mid-Atlantic Bight).

Dorsal fin rays 20–22 (Houde and Fore 1973); 17–22 (Jones et al. 1978).

Anal fin rays 20–24 (Houde and Fore 1973); 20–25 (Jones et al. 1978).

Comparative meristics for genus *Opisthonema* from Berry and Barrett (1963); ranges of values, with means in parentheses, as follows:

	Dorsal rays	Anal rays	Vertebrae
<i>O. oglinum</i>	18–22 (20.0)	22–25 (23.5)	45–49 (46.3)
<i>O. libertate</i>	17–20 (18.6)	19–22 (20.8)	44–48 (46.0)
<i>O. berlangai</i>	19–20 (19.4)	19–22 (20.7)	45–47 (46.0)
<i>O. medirastre</i>	17–20 (19.2)	19–23 (21.0)	46–48 (47.1)
<i>O. bulleri</i>	18–21 (19.6)	20–23 (21.4)	46–48 (47.0)

Larval descriptions

Gulf Egg and larval comparative information, and larval key based on literature review, wild-caught, and reared larvae (Houde and Fore 1973).

Eastern Gulf Egg and larval illustrations and descriptions of reared larvae (Richards et al. 1974).

Northwestern Atlantic Description of postlarvae and juveniles (Hildebrand 1964).

Juvenile

Reported to undergo metamorphosis at 15–25 mm (Richards et al. 1974), at 19.7 mm SL (Jones et al. 1978), and at 20–25 mm SL (Richards and Palko 1969).

Starts schooling as a juvenile, tends to school by size ($\pm 15\%$ of mean length of school) (Reintjes 1979a).

Young not abundant in estuaries or nearshore shallow waters (Arnold et al. 1960, Christmas and Waller 1973, Reintjes 1979a).

Biscayne Bay, Florida Age-1 fish, 120–130 mm (Low 1973).

Everglades, Florida Age-1 fish, 135 mm (Roessler 1967).

Florida Fish 50–67 mm FL taken in lower Boca Ciega Bay in October, fish 36–83 mm SL taken at St. Petersburg August–December with the peak in October, fish 58–102 mm taken at Fort Myers in water 17.5 ppt (Fuss et al. 1969); fish 25–100 mm FL taken in Tampa Bay July–October (Springer and Woodburn 1960); fish 61–77 mm taken at Cedar Key in September (Reid 1954); present year-round in Biscayne Bay but most abundant in summer and early fall—first caught at 25–35 mm TL (~ 1 month old) in May (Low 1973); 9645 fish taken in the Everglades in temperatures of 15.5°–34.0°C and salinities of 15.5–45.2 ppt (99% caught June–November) (Roessler 1970).

Horn Island, Mississippi In late summer and fall, 1406 fish taken (25–155 mm; most 40–90 mm), smallest fish (< 35.0 mm) taken August–October, all taken in salinities > 15 ppt and most in salinities > 25 ppt (Perry and Boyes 1978).

Louisiana Total of 89 fish (40–150 mm; $\bar{x}$ 84 mm) taken over all months except January, April, May, and June; peak occurrence in September, most fish taken in salinities > 15 ppt and temperatures of 5°–34.9°C (Perret et al. 1971).

Galveston Island, Texas One juvenile (72 mm) taken in December (Arnold et al. 1960).

Other scientific names recently used: *S. anchovia* (Fischer 1978) and *S. allecia* (Ben-Tuvia 1960b lists other synonyms).

Adult Distribution

Geographic

Western Atlantic Found from Woods Hole, Massachusetts, to Uruguay, including the Gulf of Mexico (Jones et al. 1978); Caribbean Sea, Bermuda, Bahamas, and West Indies (Klima 1971); replaced by *S. brasiliensis* off Rio de Janeiro, Brazil, and most abundant off the northern coast of Venezuela (Fischer 1978).

Eastern Atlantic and Western Pacific Found in tropical continental shelf waters bounded by 30°S and 40°N latitude (Ben-Tuvia 1960b); Adriatic Sea (de Buen 1932).

Three species of *Sardinella* in western North Atlantic (Richards et al. 1974).

Vertical (depth) or distance from shore

Florida May have an inshore as well as an offshore migration (Low 1973).

Gulf Surface and demersal schools usually associated with upwellings and increased concentrations of zooplankton; species a diurnal vertical migrator capable of migrating 60–80 m in 15–20 minutes; stays near bottom during the day (Prosvirov and Varea 1969).

Gulf and southeast U.S. Atlantic coasts Coastal pelagic species normally found within the 92-m depth contour but occasionally found in waters as deep as 366 m (Klima 1971).

Venezuela Adults live permanently on the shelf and migrate along shelf (Simpson and Gonzalez 1967).

Southeast U.S. continental shelf Adults taken in bottom trawls between 10- and 55-m isobaths; greatest collections taken 10–18 m during winter–spring and 19–27 m during summer–fall (Barans and Burrell 1976).

Mid-Atlantic U.S. Bight Usually found from surface to 100–150 m, deeper during cooler periods (Jones et al. 1978).

U.S. Atlantic coast Appears to have a north-south migration (Hildebrand 1964).

Mediterranean Non-selective planktonic feeder; does not migrate any great distances; young fish found in 18–37 m, older fish frequently taken in 27–73 m; form schools close to bottom during the day, disperse at night (Ben-Tuvia 1960b).

West Africa Species part of deep scattering layer; during cooler parts of the year schools may be very deep during the day; best harvested at night when fish migrate to the

surface (vertical migration rate of 2.0–2.5 m/min) through a temperature gradient of 6°C; also migrates horizontally or geographically with the 18°C surface isotherm (Schmidt 1972).

Schools with *Etrumeus teres* (Bullis et al. 1971), *Decapterus punctatus* (Springer 1957, Juhl 1966), *Opisthonema oglinum* (Low 1973), and *Scomber japonicus* (Reintjes 1979b).

Stock Abundance

Gulf of Mexico

Eastern Gulf Biomass not estimated, but eggs and larvae abundant (Houde et al. 1976); biomass possibly as great as that of *Opisthonema oglinum* (i.e., 250,000 t) (Houde 1977c, Houde et al. 1984); apparently a large adult population more widely distributed than those of other clupeids in the eastern Gulf; most common clupeid larvae taken (Houde et al. 1979).

Tampa, Florida Mixed school of *Etrumeus teres* and Spanish sardine 80 km offshore reported to be 80 km long, 16 km wide, and 3.7 m thick, and to occupy 6 million m³ of water (Bullis et al. 1971); found schooling with *Decapterus punctatus* in schools of 2.9–4.5 t (Juhl 1966).

Fort Myers Beach and Cape Romano, Florida Schools of 1.8–3.6 t predominate (Juhl 1966).

Other

Northern Venezuela Very abundant (Fischer 1978).

Northwestern Africa Very abundant (Sedletskaia 1972).

Fisheries

Gulf of Mexico

Gulf Soviet-Cuban fishery research identified development of this fishery as a high priority (Prosvirov and Varea 1969, Reintjes 1979a). In 1975, 46,001 t landed, 42,696 t by Venezuela, and marketed fresh or canned (Fischer 1978, Reintjes 1980).

Eastern Gulf Approximately 1–2 million t could be harvested as an aggregate catch with *O. oglinum* and *D. punctatus* and sold as bait or cat food (Houde 1975, 1977a,b,c; Reintjes 1979a, 1980).

West Florida Experimental sardine canning investigated (E.J. Conrad, Jr., Port Clyde Foods, Inc., P.O. Box 528, Rockland, ME 04841, pers. commun., Aug 1985). Significant resource potential (Bullis et al. 1971, Klima 1971); harvested for sport fishery bait, esteemed as a bait over *Opisthonema oglinum* and *Harengula jaguana* (Springer and

Woodburn 1960). Landings averaged ~363 t per year between 1960 and 1977, rising to an average of ~1247 t per year between 1978 and 1983; landings increased rapidly from 1984 (1724 t) to 1987 (2858 t) averaging ~2087 t per year (Nelson 1988).

Gulf and Caribbean Johnson and Vaught (1986) reviewed the historical fisheries and their economic potential.

Other

Venezuela, Cuba, and Brazil Harvested and canned (Bullis et al. 1971), or iced for bait in the tuna long-line fishery (Klima 1971).

Brazil One of the most important commercial fisheries (*S. brasiliensis*) (Matsuura 1971, Hubold and Mazzetti 1981).

Mediterranean Sea Adults caught in great quantities with lampara and seine nets May–November along the coast (D’Ancona 1956).

West Africa One of the most abundant and widely distributed industrial food fish (Schmidt 1972, Sedletskaya 1972).

Problems

Not readily taken with purse-seining gear; would require new and innovative harvesting systems (Juhl 1966).

Reproduction

Sexual maturity

Gulf Minimum length at sexual maturity 140–150 mm (Prosvirov and Varea 1969); 1-year-olds do not spawn; 2–3 year-olds (mean length 195 mm) are mature (Prosvirov and Varea 1969, Schmidt 1972); size at first maturity off western Florida 125 mm FL for females and 130 mm FL for males, and 50% of females not mature until 147 mm FL at an estimated mean age of 1.4 years (Grall 1984).

Venezuela Sexually mature between age-2 and age-3 (mean length ~195 mm), smallest sexually mature fish 134 mm (Heald 1966).

Mediterranean Size at sexual maturity geographically variable; off Algeria males first spawn at 120 mm and females at 135 mm; off Spain minimum size of ripe males 169 mm, and females 194 mm; off Balearic Islands minimum size of ripe males 140 mm, and females 120–130 mm (but majority of fish do not spawn until at least 160 mm); in the eastern Mediterranean male fish ripe at 120 mm and females at 125 mm (Ben-Tuvia 1960b).

Pointe-Noire, West Africa Fish attain first maturity at 210–230 mm (Rossignol 1955).

Northwest Africa First spawns at age-1 or 2 at 130–210 mm (240–320 mm at age 3–4) (Sedletskaya 1972).

Sex ratio

Gulf 1M:2F (Prosvirov and Varea 1969).

Eastern Gulf Based on 163 fish, 1.1M:1F (Houde et al. 1984).

West Florida 1.15M:1F (Grall 1984).

Venezuela Based on ~1300 fish, 1M:1.2F (Heald 1966, Heald and Griffiths 1967).

Mediterranean Sea Variation in sex ratio with size and age of fish probably caused by rapid growth of females; males predominate among fish 100–160 mm, sex ratio 1:1 for fish 120–190 mm, and females predominate in fish 160–260 mm (certainly by 200 mm) (Ben-Tuvia 1960b).

Northwest Africa Sex ratio varies 1M:1F to 2M:1F (Sedletskaya 1972).

Fecundity

West Florida Based on 25 females, batch fecundity ranged from 21,240 eggs (females 146 mm FL) to 146,729 eggs (188 mm FL), with a mean of 70,312 eggs or 871.7 eggs/g; based on 22 Atlantic females, batch fecundity ranged from 21,806 eggs (143 mm FL) to 68,044 eggs (168 mm FL), with a mean of 35,825 eggs or 778.7 eggs/g (Grall 1984).

Palm Beach, Florida Based on eight females (144–155 mm SL) taken in August 1971, fecundity ranged from 45,730 to 86,269, and mean relative fecundity was 1108 ova/g (range 637–1552 ova/g) (Martinez 1972).

Mediterranean Sea Two sizes of eggs present in ripe females; females 125–149 mm had a mean total fecundity of 13,854 (mean number of large [9757] plus small [4097] eggs), females 230–249 mm had a mean of 99,700 ova (58,300 large and 41,400 small ova), total fecundity range of 9930–113,100 ova (Ben-Tuvia 1960a).

West Africa Fecundity reportedly 10,000–270,000 ova (Martinez 1972).

Spawning season

Generally spawns 2000–2400 h; general relationship between vertical distribution of eggs and thermocline with eggs usually in mixed layer near surface (Matsuura 1971).

Spawns throughout the day, but peaks 1930–2300 h (Simpson and Gonzales 1967).

Mediterranean May spawn more than once during a season or in a series of consecutive spawnings; two size groups of ova in Mediterranean females (Ben-Tuvia 1960a).

West Florida Considered a multiple spawner; based on mean gonadal indices, spawning season April–September with a peak May–July (based on number of ripe females) and some spawning probably continuing during winter when adults migrate offshore (Grall 1984).

Everglades, southwest Florida Two specimens (19 and 21 mm SL) of *S. brasiliensis* taken in coastal waters (30.0°C and 36.7 ppt) during August; 92 specimens (4.2–17 mm SL) of *Sardinella* spp. taken in coastal waters (20.0°–29.6°C and 34.6–36.7 ppt) in depths of 6–10 m during quarterly sampling; in February (4.2–13 mm SL larvae taken) and August (11–17 mm SL) only, no *Sardinella* species taken in estuarine waters (Collins and Finucane 1984).

Eastern Gulf Protracted spawning season; eggs and larvae found in all seasons; in winter spawns only off southwestern Florida, where this species is the most common clupeid larvae taken; most eggs and larvae taken within the 10–50 m depth contour, some taken out to 100–200 m; taken in surface temperatures of 21.0°–32.0°C and salinities ≥ 35 ppt; spawns near the coast with larvae usually in the upper 10 m of the water column (Houde et al. 1976, 1979). Widely distributed along west Florida; spawns primarily in fall and winter, September–February (Houde 1973, Houde and Fore 1973).

Western Gulf Presence of larvae off the Texas coast out to the continental shelf edge indicates spawning April–October (Finucane et al. 1979).

U.S. South Atlantic Bight Total of 49 larvae taken throughout the year (Fahay 1975).

Venezuela Spawning reported year-round, but most intense during upwelling season (December–April); peak activity January–February (Simpson and Griffiths 1967, Heald 1966).

South Brazil Spawns during summer months, September–March, between 50- and 100-m depths; approximately 87% of the eggs collected at temperatures of 19°–24.9°C and salinities of >35 ppt (Matsuura 1971, 1975a).

Central Adriatic Spawns May–June and September–October; eggs found in waters 16°–21°C, larvae taken in 0–10 m depths in temperatures of 22.3°–23.9°C and salinities of 36.9–38.6 ppt (Regner 1977).

Mediterranean Sea Spawns in July and September–October (D’Ancona 1956). Eggs and larvae found summer and early autumn (May–early October, peaking July–August); spawns in upper surface waters along the coast; most eggs taken at the surface, and no larvae observed below 100 m, mean sea surface temperature of 22.2°C (Ben-Tuvia 1960b).

Northwest Africa Spawns intermittently (ovaries contain eggs of two sizes); spawning fish caught in waters 18°–27°C and >35 ppt (Sedletskaia 1972).

South Africa Has two spawning seasons, the major one May–June and secondary spawning (about one-tenth the activity of the first) October–November by younger fish; usually in salinities >35 ppt (Conand and Fagetti 1971, Conand 1981).

Eggs

General description

Eastern Gulf Pelagic eggs; embryo and yolk occupy $\sim 80\%$ of the egg capsule diameter shortly after fertilization and 60% just before hatching (Houde and Fore 1973).

Brazil Eggs spherical with thin, transparent, unsculptured membrane, spherical and irregular yolk mass (Matsuura 1971).

U.S. Mid-Atlantic Bight Eggs found from the surface to various depths, common at 5–7 m below the surface (Jones et al. 1978).

Mediterranean Sea Pelagic (D’Ancona 1956).

Matsuura (1971) and Ben-Tuvia (1960b) cite a number of papers on egg development of sardines from other regions of the world.

Egg diameter

Eastern Gulf Mean diameter 1.12 mm, range 1.03–1.25 mm (Houde and Fore 1973).

Brazil Mean diameter 1.18 mm, range 1.00–1.32 mm (Matsuura 1971); mean diameter 1.20 mm (1.00–1.40 mm) based on a total 1052 eggs over three spawning seasons (Matsuura 1975a, *S. brasiliensis*).

U.S. Mid-Atlantic Bight Mean diameter 1.10 mm, range 0.94–1.40 mm (Jones et al. 1978).

Central Adriatic Mean diameter 1.24–1.31 mm (1.13–1.43 mm; $N=140$) (Regner 1977).

Mediterranean Sea Diameter 1.20–1.40 mm (D’Ancona 1956, Ben-Tuvia 1960b); mean diameter 1.16 mm (1.01–1.32 mm) off the Balearic Islands (Oliver and Navarro 1952).

Perivitelline space

Eastern Gulf Moderate, 20–40% of egg diameter (Houde and Fore 1973).

Brazil Wide, mean width 0.14 mm (0.06–0.25 mm) (Matsuura 1971).

U.S. Mid-Atlantic Bight Wide, mean width 0.29 mm (Jones et al. 1978).

Mediterranean Sea Large (D’Ancona 1956, Ben-Tuvia 1960b).

Oil globule

Eastern Gulf One, diameter 0.13–0.18 mm (Houde and Fore 1973).

Brazil Usually one oil globule (mean diameter 0.14 mm; range 0.09–0.18 mm), but may have two or three (Matsuura 1971).

U.S. Mid-Atlantic Bight Usually one large oil droplet (mean diameter 0.14 mm; range, 0.12–0.16 mm) with several (usually three) small ones 0.08–0.09 mm (Jones et al. 1978).

Mediterranean Sea One oil droplet (mean diameter 0.12 mm), usually yellow (D'Ancona 1956, Ben-Tuvia 1960b).

Central Adriatic Sea One droplet (mean diameter 0.11–0.13 mm; range 0.08–0.15 mm; $N=138$ eggs) (Regner 1977).

Incubation time

In subtropical and temperate zones, hatching time of ~2–4 days (e.g., Japanese sardine hatches in 38–50 h in waters 17.5°–20.3°C) (Matsuura 1971).

In waters 21.4°–23.4°C, 24 h (Matsuura 1975a, *S. brasiliensis*).

Larvae

Hatching length

Western North Atlantic and northwest Africa Recently hatched larvae ~3.0 mm (Fahay 1983, western North Atlantic; Sedletskaia 1972, northwest Africa).

Egypt Larvae 2.3 mm TL (Whitehouse 1933).

Early-life-history information

Israel Larval growth rate of 0.60 mm/d during the first month after hatching, assuming daily growth increments in otoliths (Walline 1987).

South Africa Larvae reported to be cannibalistic (Conand 1981).

Meristics

Myomeres 48 (Houde and Fore 1973, eastern Gulf; D'Ancona 1956, Gulf of Napoli); postdorsal-preanal myomeres 5–7 (Houde and Fore 1973), 5–8 (Fahay 1983, western North Atlantic); predorsal myomeres decrease from 28 to 24 (Fahay 1983); vertebrae 45–47 (Wongratana 1980, Indo-Pacific).

Dorsal rays 16–17 (Prosuirov and Varea 1969); 16–19 (Houde and Fore 1973); 17–20 (Wongratana 1980).

Anal rays 16–18 ($\bar{x}$ 17) (Prosuirov and Varea 1969, Gulf); 16–17 (Houde and Fore 1973); 16–18 (Wongratana 1980).

Pelvic fins have nine branching rays, not eight like many other *Sardinella* spp. (Prosuirov and Varea 1969, Wongratana 1980).

Caudal rays 15 at 11 mm (Jones et al. 1978, Mid-Atlantic Bight).

Larval descriptions

Eastern Gulf Egg and larval illustrations, comparative information, and larval key based on a literature review and lab-reared and wild-caught larvae (Houde and Fore 1973).

Northeastern Venezuela Egg illustrations and description of wild-caught specimens (Simpson and Gonzalez 1967).

Mediterranean Sea Egg and larval illustrations of wild-caught specimens (Fage 1920).

Adriatic Sea Egg and larval illustrations of wild-caught specimens (D'Ancona 1956, reproduced from Raffaele 1888).

Egypt Illustrations (Whitehouse 1933, cited in Jones et al. 1978).

South Africa Illustrations and comparative information on *S. aurita* and *S. eba* from wild-caught specimens (Conand and Fagetti 1971).

Brazil *S. pseudohispanica* and/or Spanish sardine (Abousouan 1969).

South Brazil *S. brasiliensis* (Matsuura 1971, 1975b).

Madras Coast *S. longiceps* (Nair 1959).

Juvenile

Transforms at ~25 mm TL (Fahay 1983).

Mediterranean Sea Metamorphosis complete at 30 mm TL, less than a month old (Ben-Tuvia 1960b).

Biscayne Bay, Florida Juveniles (40–50 mm) first caught in May and June in shoreline grassbeds (Low 1973).

Tampa Bay, Florida Five juveniles (44.0–54.0 mm) taken November, ten fish (61.2–77.0 mm) taken December, large school (50–60 mm) taken June, seven fish (63.2–77.0 mm) taken July (Springer and Woodburn 1960).

Eastern Gulf Mean length of age-1 fish, 130 mm; age-2 (1+) fish, 135–172 mm ($\bar{x}$ 170 mm); age-3 (2+) fish, 162–200 mm (Prosuirov and Varea 1969).

Alabama estuaries One “juvenile” (121 mm) taken during August (Swingle 1971).

Venezuela *Annulus* *dens* late February-March; mean length by first annulus formation, 138 mm; by second annulus formation, mean length 167 mm; by third annulus formation, mean length 190 mm (Heald 1966; Heald and Griffiths 1967).

Adriatic Sea Juveniles (35-45 mm) caught in abundance in seine nets October-November (D'Ancona 1956).

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CONTENTS OF MANUSCRIPT

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